

ON THE SYSTEMATICS OF *TRICHIA* S. LAT.  
(PULMONATA: HELICOIDEA: HYGROMIIDAE)

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ABSTRACT

Systematic revision of Asiatic, Caucasian and some European species of the *Trichia* s. lat. group of the Trichiinae has shown that it is not a united genus but a complex of genera. All known representatives (8) of the Central Asian group, all species but 1 occurring in the Caucasus (14), and 9 representatives of the main European taxa are treated in the Systematic Part (31 species). The anatomical investigation comprises 29 species, including 25 of the 27 species known in the USSR. Of the 9 genera recognized, 3 are new: *Hygrohelicopsis*, *Teberdinia*, *Plicuteria*, and also 4 species: *Leucozonella caria*, *Hygrohelicopsis darevskii*, *Kokotschashvilia tanta*, *K. eberhardi*.

Apart from shell and traditional anatomical characters, great attention has been paid to peculiarities of the inner structure of the genitalia. It was thus found that *Hygrohelicopsis darevskii* does indeed possess 2 pairs of dart sacs, though the inner pair is not visible from the outside. In this species the right ocular retractor does not pass between penis and vagina, as in *Trichia*, but only near them, which is considered to be characteristic for *Helicopsis* in the "Helicellinae" auct.; but from the totality of other characters *Hygrohelicopsis* is nevertheless regarded as belonging in the Trichiinae. *Teberdinia* was found to differ from other Caucasian forms by having a deep longitudinal groove on the surface of the penis papilla that separated off a lobe and from all other forms by having one of the intrapapillar cavities reaching into this lobe. In the genus *Plicuteria* the longitudinal vaginal plicae are subdivided by regular transverse prismatic folds forming a unique dense pattern on the internal wall of the vagina. *Kokotschashvilia tanta* and *K. eberhardi* can be distinguished, among other features, by the structure of the inner wall of the penis papilla, which in the latter is not smooth but plicate.

The Asiatic group is distinguished from the European-Caucasian group by the mode of formation of the intrapapillar cavity or cavity system. In the former group it arises from the closing of a groove on the surface of the verge, the main phases of the process being evident in the material studied. In the latter group the cavities arise as paired structures in the thickness of the papillar wall and then assume more complex forms. The proposed new systematics of the *Trichia* s. lat. group are based on various characters of a different nature, taking into consideration as far as possible the organization of the animal as a whole, as only such an analysis can reflect on the evolution of the various groups and the true relations among them.

INTRODUCTION

The use of gross genital morphology in stylommatophoran pulmonates has helped our understanding of systematics at the family level. Findings reflect relationships as they have evolved in nature. In practice, however, this approach has sometimes re-

sulted in the creation of large genera comprising the anatomical characters of the many species included. One result is that the conchological features of such genera have become so hazy as to be quite useless.

The genus *Trichia* s. lat. (Trichiinae)<sup>2</sup> is very interesting in this respect. A conchological diagnosis of the group is not practi-

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<sup>2</sup>The author, replacing a classification that recognizes 2 subfamilies, the Hygromiinae and Helicellinae, subdivides (Shileyko, 1972) the family Hygromiidae Tryon, 1866, into 7 subfamilies:

Trichiinae Zilch & Jaeckel, 1962

Hygromiinae Tryon, 1866

Metafruticicolinae Shileyko, 1972

Monachinae Zilch, 1960

Cochlicellinae Shileyko, 1972

Ciliellinae (?) Shileyko, 1972

Geomitrinae Wenz, 1923

The "Helicellinae" auct. are not considered to form a natural group but to consist of various hygromiid "vital forms" (Shileyko, 1972: 28-41).

cable. The only diagnostic feature is the presence of 2 pairs of symmetrically situated dart sacs (stylophores). Other anatomical characters such as the shape and relative length of the flagellum, epiphallus, penis and spermathecal duct; the shape of the receptaculum seminis (spermatheca) and of the vagina; the number, location and nature of mucous glands and of their branches; and the presence of bends in the free oviduct are rather variable, and none of them is constant within the whole group. But one anatomical feature allows us to separate the present group from species of the genus *Helicopsis*, which belongs in the "Helicellinae" auct.: the right ocular retractor passes between the penis and vagina, not merely close to them, as in *Helicopsis*. This feature and its taxonomic value will be discussed in more detail below.

The present paper shows that the genus *Trichia* is more complex than hitherto imagined. The probable phylogenetic relationships in the genus complex will be discussed after a systematic review of the species studied.

This study includes the majority of species known from the USSR and also some eastern and central European forms allied to those from the European part of the Soviet Union. A total of 31 species that fall into 9 genera were considered as follows; 2 of these, marked by asterisks, were not examined.

- Genus *Odontotrema* Lindholm, 1927  
*O. diplodon* Lindholm, 1927
- Genus *Leucozonella* Lindholm, 1927  
*L. ferghanica* Lindholm, 1927  
*L. caryodes* (Westerlund, 1896)  
*L. rubens* (Martens, 1874)  
*L. mesoleuca* (Martens, 1882)\*  
*L. rufispira* (Martens, 1874)  
*L. retteri* (Rosen, 1897)  
*L. caria* Shileyko, sp. nov.
- Genus *Hygrohelicopsis* Shileyko, gen. nov.  
*H. darevskii* Shileyko, sp. nov.
- Genus *Teberdinia* Shileyko, gen. nov.  
*T. zolotarevi* (Lindholm, 1913)
- Genus *Kokotschashvilia* Hudec & Lezhawa, 1969  
*K. makvalae* (Hudec & Lezhawa, 1969)  
*K. tanta* Shileyko, sp. nov.  
*K. holotricha* (Boettger, 1884)  
*K. eberhardi* Shileyko, sp. nov.  
*K. phaeolaema* (Boettger, 1886)
- Genus *Caucasigena* Lindholm, 1927  
 Subgenus *Caucasigena* s. str.

- C. (C.) armeniaca* (L. Pfeiffer, 1846)  
*C. (C.) tschetschenica* (Retowski, 1914)  
*C. (C.) rengarteni* (Lindholm, 1913)  
*C. (C.) eichwaldi* (L. Pfeiffer, 1846)  
*C. (C.) abchasica* (Lindholm, 1927)\*
- Subgenus *Anoplitella* Lindholm, 1929  
*C. (A.) schaposchnikovi* (Rosen, 1911)
- Subgenus *Dioscuria* Lindholm, 1927  
*C. (D.) thalestris* (Lindholm, 1927)
- Genus *Plicuteria* Shileyko, gen. nov.  
*P. lubomirskii* (Ślóssarski, 1881)
- Genus *Trichia* Hartmann, 1840  
 Subgenus *Petasina* Beck, 1847  
*T. (P.) unidentata* (Draparnaud, 1805)
- Subgenus *Trichia* s. str.  
*T. (T.) plebeia* (Draparnaud, 1805)  
*T. (T.) concinna* (Jeffreys, 1862)  
*T. (T.) hispida* (Linneé, 1758)  
*T. (T.) villosula* (Rossmäessler, 1838)  
*T. (T.) striolata* (C. Pfeiffer, 1828)  
*T. (T.) danubialis* (Clessin, 1874)
- Genus *Edentiella* Polinski, 1929  
*E. bakowskii* (Polinski, 1924)

This material was collected from the following geographical areas (Fig. 1): *Odontotrema* and *Leucozonella* from Central Asia west of the great Tian-Shan Mountains (Fig. 2); *Hygrohelicopsis*, *Teberdinia*, *Kokotschashvilia* and *Caucasigena* from the Caucasus (Fig. 3); *Plicuteria*, *Trichia* and *Edentiella* from various European countries (Fig. 4).

#### SYSTEMATIC PART

In the following text, shell descriptions are given only for the little-known, rare or new species. The details of internal anatomy are mostly those relevant to taxonomic analysis. The characters of proximal reproductive structures do not distinguish genera and species; therefore the ovotestis, spermoviduct and albumen gland are not described.

The terminology of the features of the reproductive tract is not uniform in the literature, and some features have not been previously used in taxonomic distinction;

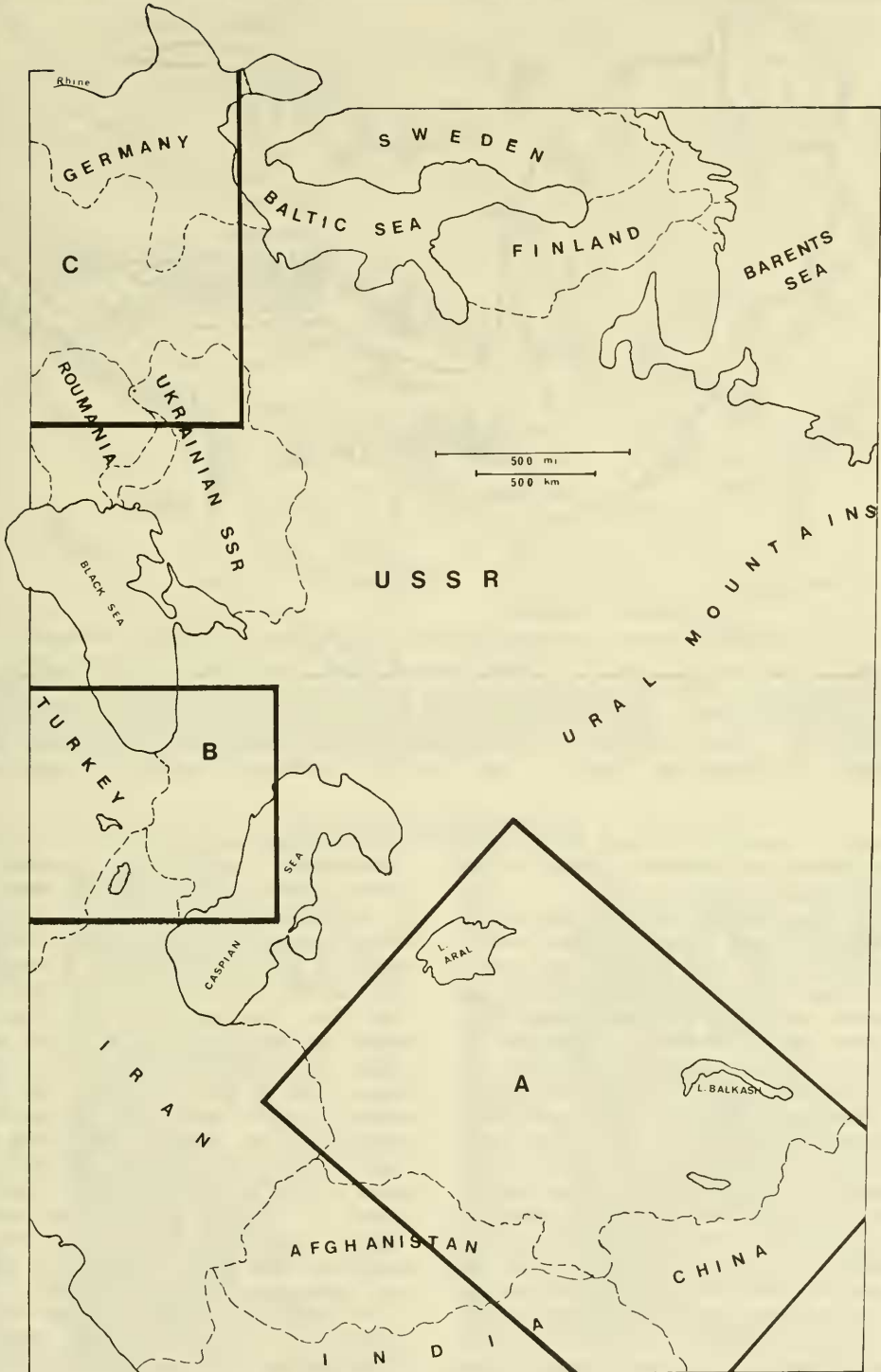


FIG. 1. Map showing the 3 general areas in which the species discussed were collected.

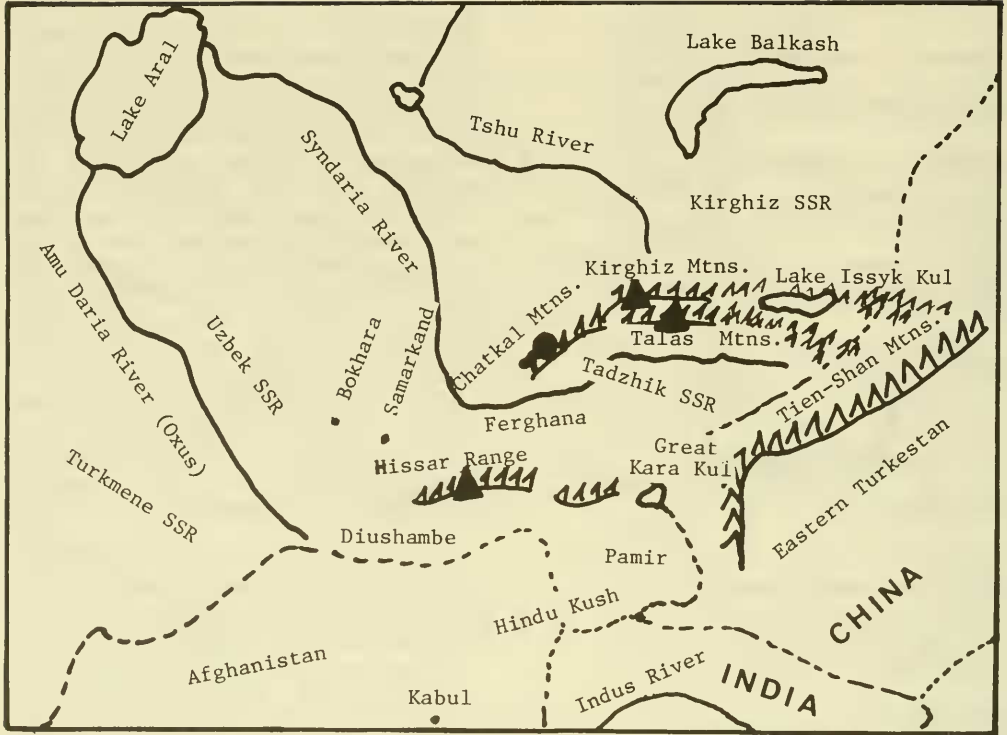


FIG. 2. Inset A of Fig. 1, the source area of central Asian specimens. This map shows the locations of Central Asian *Trichia* s.l. collected in the Soviet Union (in the Kirghiz, Chatkal, Talas, and Hissar Mountains, i.e., in the western spurs of the Tien-Shan Mountains. Black circles = *Odontotrema*; black triangles = *Leucozonella* spp. Note: kul = lake; Uzbek SSR = Uzbekistan; Tadzhik SSR = Tadzhikistan, etc.

therefore, certain terms used in this paper are defined and attention is drawn to particular features.

The free oviduct, i.e., that part of the female tract that continues the oviduct or uterine part of the spermatheca, which runs from the point of departure of the vas deferens to that of the spermathecal duct, is here called "oviduct"; "bend of the oviduct" is used in specific differentiation. The following part of the tract, the vagina, is subdivided into an upper and lower portion: the upper lies in the mucous gland region above the dart sacs, and the lower included the dart sacs and continues to the genital atrium. The "dart sacs," which are accessory organs, are either rudimentary or contain lime shafts; "stylophore" is perhaps a shorter and more exact term for dart sac.

In the distal part of the male genital tract several features have been accorded special attention. The penis consists of the "penis sheath" and "papilla" ("verge"). Inside the walls of the inner verge surround-

ing the seminal canal we find one or more "intrapapillary cavities," i.e., a system of cavities, some of which may be separated by longitudinal tissue bands or by longitudinal septa. These communicate with the cavity of the penis sheath by a foramen, the "papillary lacuna" (or by several lacunae). The "papillary plicae," or folds, are ridges on the inner surface of the penis sheath. A "connective tissue penial membrane," i.e., a thin membrane that may contain muscle fibers, may be stretched among the vas deferens, epiphallus and penis. Between the epiphallus and the distal parts of the penis sheath there may be groups of muscle fibers, here termed "penial muscle bands," either alone or associated with bands of connective tissue, the "connective tissue penial bands."

The term "perspective" applied to the umbilicus or perforation of the shell denotes that the whorls can be seen in widely or narrowly umbilicate or even perforate shells.





FIG. 3. Inset B of Fig. 1, the source area of specimens from the Caucasus. The locations of Caucasian *Trichia* s.l. collected in the Soviet Union. Open square = *Teberdinia*; black square = *Caucasigena* spp.; open triangle = *Kokotschashvilia* spp.; black triangle = *Hygrohelicopsis*. The crosses indicate that exact localities are not known but are located by district only.

## LIST OF ABBREVIATIONS

|      |                                   |      |  |
|------|-----------------------------------|------|--|
| AIG  | albumen gland                     | P    | penis  |
| BO   | bend of oviduct                   | PF   | penial folds (plicae)  |
| CML* | central mantle lobe               | PGr  | papillar groove (intrapapillar cavity that still remains open) |
| CPB  | connective tissue penial band     | PL   | papillar lacuna  |
| CPM  | connective tissue penial membrane | PMB  | penial muscle band   |
| D    | dart (stylet)                     | PP   | penis papilla (verge)  |
| DS   | dart sac (stylophore)             | Pr   | prostate   |
| EDS  | outer (external) dart sac         | RML* | right mantle lobe  |
| Ep   | epiphallus                        | ROT  | right ocular retractor   |
| F    | flagellum                         | RP   | retractor (muscle) of penis                                    |
| GA   | genital atrium                    | SC   | seminal canal (duct)   |
| HD   | hermaphrodite duct                | SD   | spermathecal duct  |
| IA   | intrapenial appendix              | SIC  | septa in intrapapillar cavity                                  |
| IC   | intrapapillar cavity              | SOD  | spermoviduct   |
| IDS  | inner (upper) dart sac            | Sp   | spermatheca  |
| LML* | left mantle lobe                  | V    | vagina (lower portion)   |
| MFE  | main folds of epiphallus          | VD   | vas deferens   |
| MG   | mucous glands                     | VF   | vaginal folds (plicae)   |
| Ov   | oviduct                           |      |  |

\*The mantle collar and its lobes have been figured for some species, for what it is worth, but the feature is not further discussed as the material is not sufficient for any conclusions.

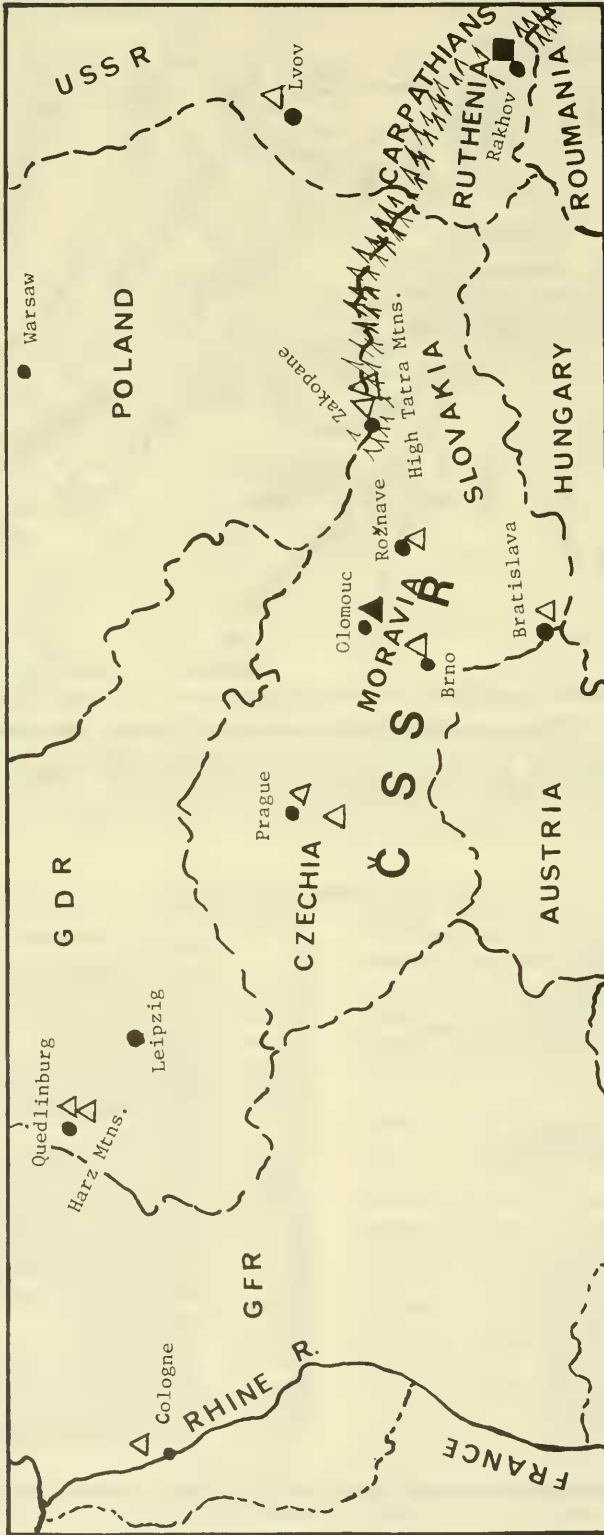


FIG. 4. Inset C of Fig. 1, the source area of European specimens. Black square = *Edentella*; open triangles = *Trichia* spp; black triangle = *Plicuteria*. CSSR = Czechoslovakia; GDR = German Democratic Republic; GFR = German Federal Republic.

Genus *Odontotrema* Lindholm, 1927

The shell is lowly conical with a smooth angle on the periphery; it is finely hirsute and brown. The umbilicus is relatively wide and perspective. There is a fine lip in the aperture on which there are 2 teeth: a larger basopalatal tooth and a basocolumellar one. The dart sacs are club-shaped and weakly fused together. There are 4 unbranched mucous glands. The inner surface of the penis sheath is covered with clear-cut, fluted ridges; the surface of the verge bears a longitudinal groove. There are no cavities in the verge walls. The flagellum is a little shorter than the epiphallus.

Genus monotypic.

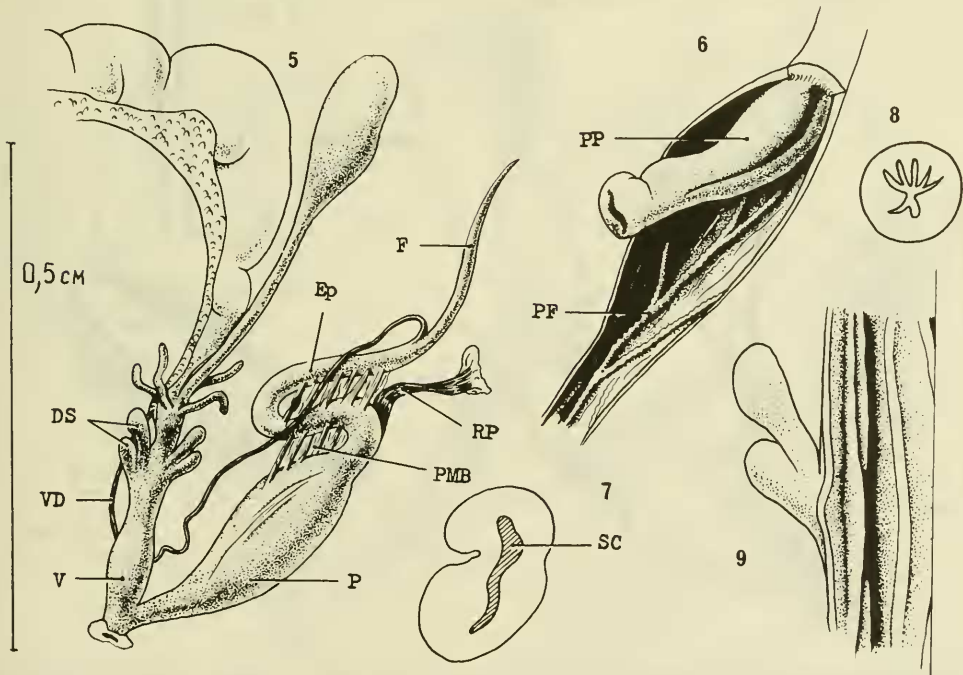
*Odontotrema diplodon* Lindholm, 1927

Figs. 5-9; Pl. I, 1

Two specimens were examined. These were collected from the scree at the base of the Chatkal Range, NW Tian-Shan Mountains, Kirghiz SSR, central Asia, in May 1972, and identified by me.

The characteristic features of the internal anatomy are as follows. The oviduct

(uterus) part of the spermoviduct passes straight into the free oviduct without any curve. The 4 mucous glands are simple, nonbranching and radially arranged. The dart sacs are thin and long, the inner dart sacs fused with the outer at their base; the inner dart sacs are almost free of the vagina. The lower vagina is long, fusiform; slight longitudinal plicae run within the whole of the inner vagina, the "vaginal plicae." At the outlet of the dart sacs these plicae form in distinct lobes. The flagellum is shorter than the epiphallus; the latter curves twice and is held in this position by connective tissue bands containing muscle fibers. The penis is relatively very massive, fusiform; its inner surface bears branching, slightly crimped, long ridges. The verge is generally cylindrical, with a long, deep groove which disappears distally. The distal part of the verge is constricted by an incomplete circular groove. Except for the vas deferens (seminal canal), the verge does not contain any cavities. There are some long, weak connective tissue bands on the surface of the penis sheath. The spermathecal duct (truncus receptaculi) has no abrupt curves and passes smoothly to the elon-



FIGS. 5-9. *Odontotrema diplodon* Lindholm, Chatkal range, NW Tian-Shan Mountains, Kirghiz SSR, May 1972. 5, reproductive tract; 6, penis, penis sheath partly removed; 7, cross-section of verge; 8, cross-section of epiphallus; 9, inner structure of vagina in dart sac region.

gate-oval spermatheca (receptaculum seminis), which nearly reaches the lower edge of the albumen gland.

Genus *Leucozonella* Lindholm, 1927

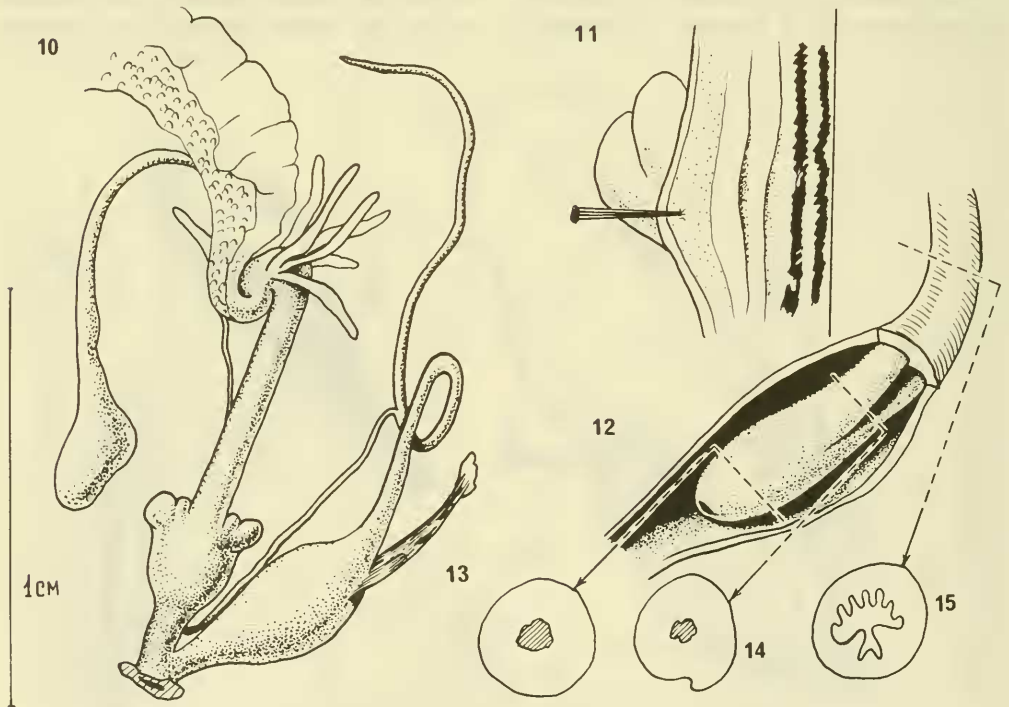
The shell is globose to lowly conical; in the latter case it may be angular at the periphery. Its color varies from light gray, yellowish, reddish to brown; on the periphery there is a light line, which is sometimes very faint. The umbilicus may vary from dot-like to relatively wide. Sometimes it is half covered by the reflected columellar edge of the aperture. The dart sacs are globose or elongate. There are 3 or 4 mucous glands, having 2-3 branches. The inner surface of the penis sheath is smooth. The verge has a long groove, developed to various degrees, or it is closed, forming an intrapapillar cavity.

Type-species: *Helix rubens* Martens, 1874.

*Leucozonella ferghanica* Lindholm, 1927  
Figs. 10-15; Pl. I, 2

Two specimens were examined. They were collected in the Sary-Chileck Nature Reserve near Lake Kula-Kul, Chatkal Range, NW Tian-Shan Mountains, Kirghiz SSR, on 6 July 1966, by A. J. Jankowskaja and identified by I. M. Likharev. A description of the shell is given by Likharev & Rammelmeyer (1952).

The oviduct forms 2 sharp bends, and the walls of the tube are tightly pressed together (Fig. 10). The length of the straight part of the tube, the upper vagina, from the bend to the dart sacs, is 6-7 times its width. The dart sacs are globose; the sac region is separated from the lower vagina by a slight narrowing. The flagellum is thin, slightly longer than the epiphallus. The penis is very bulbous, fusiform. The verge bears a groove on its basal part (Figs. 12-14). The spermathecal duct is almost



FIGS. 10-15. *Leucozonella ferghanica* Lindholm, Sary-Chileck Nature Reserve, Chatkal range, NW Tian-Shan Mountains, Kirghiz SSR, 6 July 1966. 10, reproductive tract; 11, inner structure of vagina in dart sac region; 12, penis, penis sheath partly removed; 13, 14, cross-sections of verge at different levels; 15, cross-section of epiphallus.

straight and ends in a small spermatheca nearly spherical in form, which almost reaches the albumen gland.

*Leucozonella caryodes* (Westerlund, 1896)  
Figs. 16-20; Pl. I, 3

Four specimens were examined. I collected them from the Talas Range, NW Tian-Shan Mountains, Kirghiz SSR, on 4 June 1972, and identified them.

This species differs from *L. rubens* by its shell, which has considerably thicker walls and a narrower umbilicus (see Pl. I, 3b and 4b).

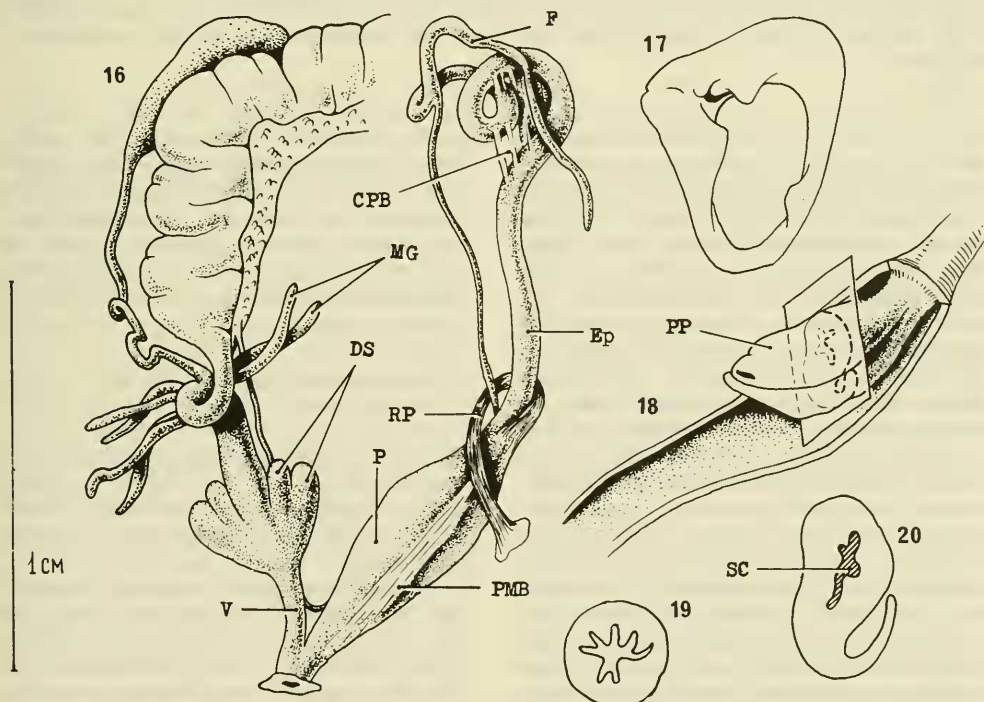
The oviduct forms a loop-like bend (Fig. 6). Usually there are 3 mucous glands, each with 2 branches. The distance between the basal part of the mucous glands and the upper limit of the dart sacs is approximately equal to the length of the lower vagina. The dart sacs are not globose but elongate, almost club-shaped. The lower vagina is thin; it is 2.5-4 times longer than it is wide. Vaginal plicae are very massive. The lobes at the outlet of the dart sac ducts are not well expressed. The flagellum

is long, longer than the fine, curved, cylindrical epiphallus. The different portions of the epiphallus are connected by short connective tissue bands (CPB, Fig. 16); there are also longitudinal muscle bands (PMB) on the surface of the fusiform penis. The inner surface of the penis sheath is smooth. The verge bears a sharp, long groove, the plane of which forms an acute angle with the sagittal papilla plane (Figs. 18, 20). The penis retractor loops around the epiphallus. The spermathecal duct is thin and slightly curved and merges indistinctly with the elongate-oval receptaculum seminis. The latter does not quite reach the albumen gland.

*Leucozonella rubens* (Martens, 1874)  
Figs. 21-26; Pl. I, 4

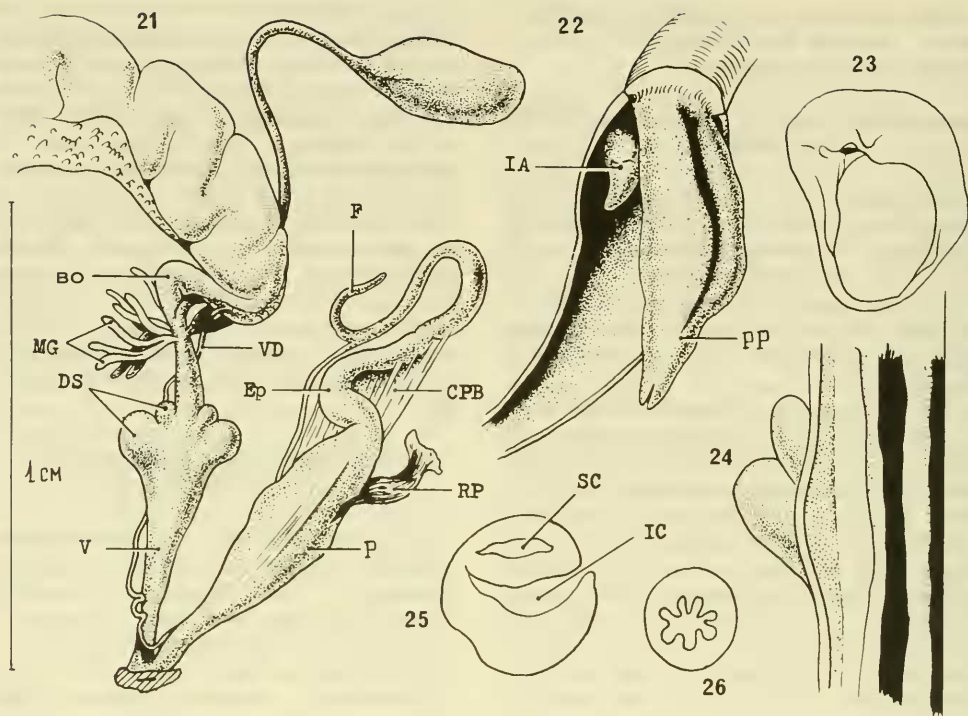
Five specimens from the foothills of the Kirghiz Range (formerly Alexander Mountains), NW Tian-Shan Mountains, Kirghiz SSR, were examined; collection (15 June 1972) and identification are mine.

This shell is very much like that of "*Euomphalia*" *regeliana*" (Martens, 1882)



FIGS. 16-20. *Leucozonella caryodes* (Westerlund), Talas range, NW Tian-Shan Mountains, Kirghiz SSR, 4 June 1972. 16, reproductive tract; 17, mantle collar with 3 lobes; 18, penis, penis sheath partly removed; 19, cross-section of epiphallus; 20, cross-section of verge.





FIGS. 21-26. *Leucozonella rubens* (Martens), foothills of the Kirghiz range, NW Tian-Shan Mountains, Kirghiz SSR, 15 June 1972. 21, reproductive tract; 22, penis, penis sheath partly removed; 23, mantle collar; 24, inner structure of vagina in dart sac region; 25, cross-section of verge; 26, cross-section of epiphallus.

(cf. Pl. I, 4a, b, c and Pl. II, 5a, b, c); the shell of the latter species has a narrower umbilicus and in this respect it resembles *L. caryodes*, but it differs from it by being thinner. Nevertheless, despite these differences among the 3 species, positive identification is possible only after dissection.

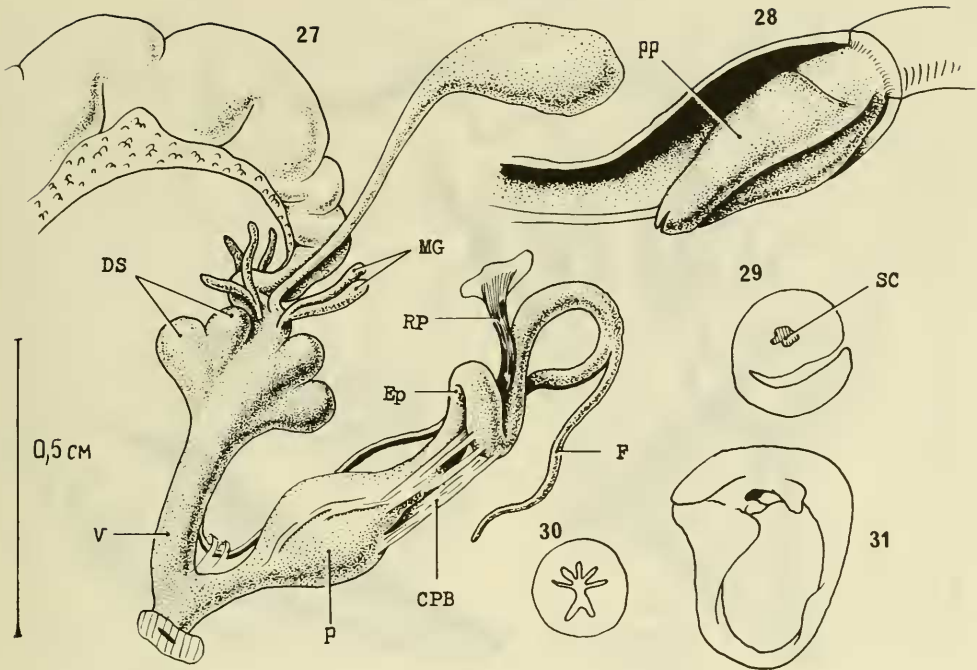
The oviduct is rather narrow and long and bends suddenly (Fig. 21). There are 3-4 mucous glands, situated considerably higher than the dart sacs; each gland has 2-5 branches. The outer dart sacs are considerably larger than the inner ones; all are nearly spherical. The dart sac region tapers toward the vagina without any sudden narrowing. The vaginal plicae as well as the lamellae on them are indistinct. The flagellum is 2/5 to 1/4 the length of the epiphallus. The penis is fusiform to globose; the inside of the penis sheath is smooth, without any folds or lamellae. The verge bears a narrow, sharp, deeply incised groove on its surface. At the base of the papilla there is an appendix (IA, Fig. 22), developed to various degrees, in the form of a protuberance, of a conical callus or (when maxi-

mally developed) of a spongy lamina, partly superimposed upon the papilla. There is a connective tissue membrane between the penis and the epiphallus in this species. The spermathecal duct is thin and rather long; it ends in an oval spermatheca that reaches the lower edge of the albumen gland.

*Leucozonella rufispira* (Martens, 1874)  
Figs. 27-31; Pl. II, 6

Four specimens were examined. They were collected from the Anzob Pass, Hissar Range, W Tian-Shan Mountains, Tadzhik SSR, on 28 July 1968, by Z. Izzatulaeva and identified by him.

The oviduct forms a sudden bend, with the inner walls touching. As a rule there are 3-4 mucous glands sited around the upper vagina, all usually having 2 branches. The dart sacs are very massive and spherical, and the inner ones are not as short as the outer ones. The length of the lower vagina exceeds its width 3-4 times. The vaginal plicae are rather clear and show



FIGS. 27-31. *Leucozonella rufispira* (Martens), Anzob pass, Hissar Range, W Tian-Shan Mountains, Tadzhik SSR, 28 July 1968. 27, reproductive tract; 28, penis, penis sheath partly removed; 29, cross-section of verge; 30, cross-section of epiphallus; 31, mantle collar.

distinct laminae. The flagellum is a little shorter than the sharply curving and slightly coiling epiphallus. The loop of the epiphallus is drawn to the penis sheath by connective tissue bands (CPB, Fig. 27). The penis is globose, and the inner surface of its sheath is smooth. The verge is fusiform and has a very deep, long, longitudinal groove. In addition, there is a transverse groove not wholly encircling the proximal part of the papilla. The papilla wall has no cavities. The spermathecal duct is thin and almost straight, ending in an oval receptaculum seminis and stopping considerably short of the lower edge of the albumen gland.

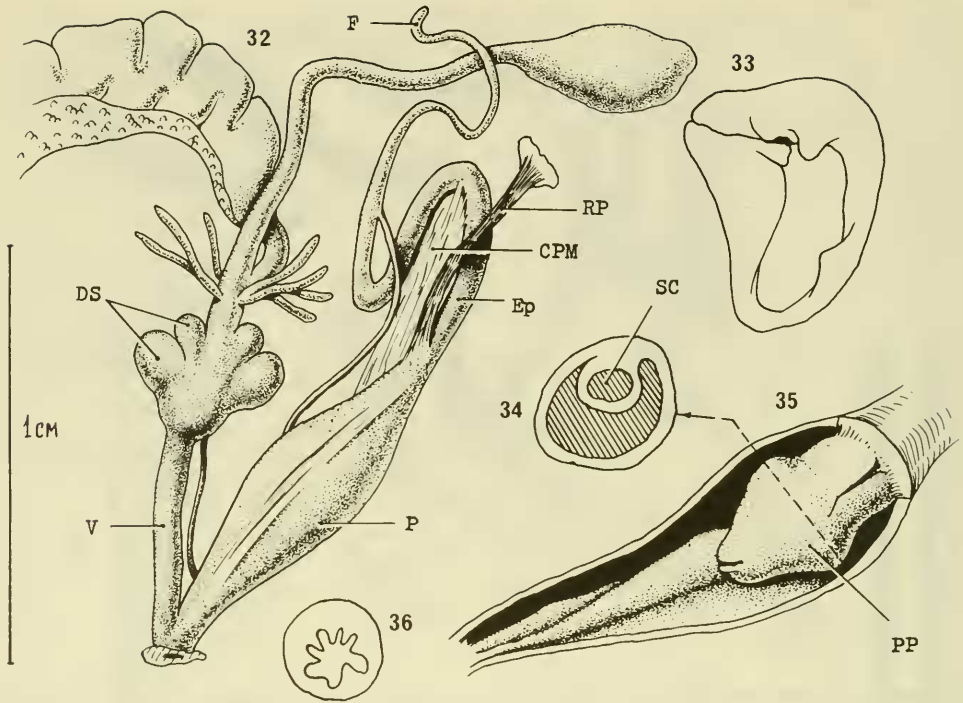
Our observations differ somewhat from those of Likharev & Starobogatov (1967). According to these authors, there are 2 mucous glands on the very bend of the oviduct and the flagellum is  $2/5$  the length of the epiphallus.

*Leucozonella retteri* (Rosen, 1897)  
Figs. 32-36; Pl. II, 7

Four specimens were examined; they were collected in Kandara Valley, Hissar

Range, W Tian-Shan Mountains, Tadzhik SSR, on 2 July 1967, by Z. Izzatulaev and identified by him.

The oviduct forms only a slight bend. There are 4 mucous glands; they usually have 2 branches (1 specimen had 1 simple gland, Fig. 32). The dart sacs are massive, inflated, globose. The lower vagina is set off from the region of the dart sacs by a marked narrowing; it is long, narrow and cylindrical; its length is 5-6 times its width. The vaginal plicae are not distinct and form clear-cut lobes only at the entrance of the dart sacs. The flagellum is about as long as the epiphallus; the latter curves twice. There is a connective membrane between penis and epiphallus (CPM, Fig. 32); connective tissue bands also run along the penis sheath surface. The penis is massive, fusiform. The verge has a characteristic shape: its proximal part is cylindrical; it then suddenly widens out and ends in a conical distal part (Fig. 35). The seminal duct is fused to one side of the inner papilla wall, and it is embraced on all other sides by a vast intrapapillar cavity. A heavy crest-shaped plica runs on the inner surface of the penis. The spermathecal duct is



FIGS. 32-36. *Leucozonella reteri* (Rosen), Kandara Valley, Hissar Range, W Tian-Shan Mountains, Tadzhik SSR, 2 July 1967. 32, reproductive tract; 33, mantle collar; 34, transverse section of papilla showing single intrapapillar cavity with crescent-shaped cross-section; 35, penis, penis sheath partly removed; 36, cross-section of epiphallus.

slightly curved; an oval spermatheca reaches the lower edge of the albumen gland.

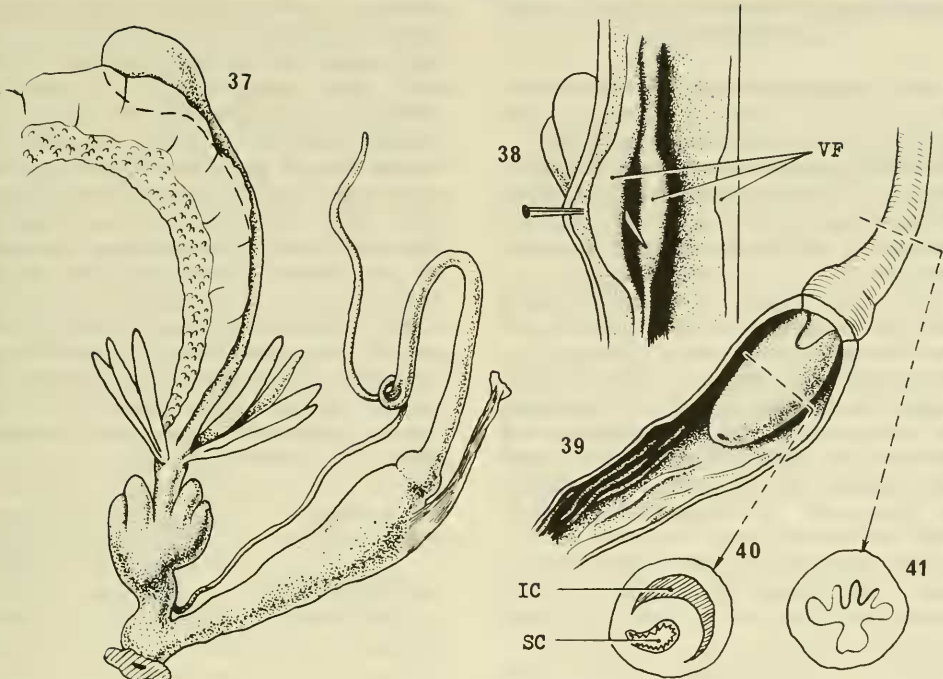
*Leucozonella caria* Shileyko, sp. nov.  
Figs. 37-41; Pl. II, 8

Three specimens from the Hissar Range, W Tian-Shan Mountains, Tadzhik SSR, at the outskirts of the Khodzcha-Obi-Garm Rest Home, were examined. They were collected on 28 May 1968 by Z. Izzatuliev and identified by me. The holotype is at the Zoological Institute, USSR Academy of Sciences, Leningrad.

The shell is small (8-9 mm) and very much like that of the European *Trichia* s. str., but it has a constant distinction: it has no more than 4.5-5 whorls, whereas in fully adult *Trichia* s. str. there usually are 6 whorls. The shell may vary in aspect from lowly conical to nearly conical; it is brownish-horny with a washed-out light line at the periphery. It is sculptured with fine and rather light radial lines. The body whorl is 1.5 times wider than the penulti-

mate whorl. The shell is covered with long periostracal hairs, curved at the ends as in *Trichia plebeia*. When the hairs are lost, marks are left in their place that look like short radial wrinkles. Spiral sculpture is absent. The nuclear whorls are glossy and not clearly limited from the adult whorls, and they have the same color. The whorls increase rather slowly in size, though more rapidly than European *Trichia*. The aperture is rounded inside; slightly away from the edge there is a low but wide, light-colored lip, which occupies the whole edge of the aperture in adults and is not limited to the basal part only. The umbilicus is narrow but perspective; though the columellar edge of the aperture is slightly reflected, it does not cover the umbilicus. The aperture is not deflected, moderately oblique. Measurements are as follows:

|              | Holotype<br>(mm) | Paratype<br>(mm) |
|--------------|------------------|------------------|
| Shell height | 4.7              | 6.0 4.2          |
| Shell width  | 7.8              | 8.8 7.7          |



FIGS. 37-41. *Leucozonella caria* Shileyko, sp. nov., holotype, Khodzcha-Obi-Garm Rest Home, Hissar Range, W Tian-Shan Mountains, Tadzhik SSR, 28 May 1968. 37, reproductive tract; 38, inner structure of vagina in dart sac region; 39, penis, penis sheath partly removed; 40, cross-section of verge; 41, cross-section of epiphallus.

The shell of *L. caria* can be distinguished from that of *L. reitteri* not only by its small size but also by its color and texture: *L. reitteri* is light brown to reddish and has no hairs. In the structure of the verge, *L. caria* is characteristic for the Asiatic group and sharply differentiated from the European *Trichia* (cf. Fig. 160, IV, V).

The oviduct is short and does not form a bend; there are 3 mucous glands, each with 2 or 3 branches. These are long, 1.5-2 times longer than the upper vagina. The dart sacs are relatively very massive, elongate; the outer sacs are closely pressed to the inner ones. The lower vagina is straight or curved. The flagellum is fine, not as short as the epiphallus, which forms a curve. The penis is elongate; between epiphallus and penis there is a ring-like swelling (bulla). The verge is small and oval and does not measure more than half the penis length. The intrapapillar cavity is as in *L. reitteri*: it embraces the seminal duct, which adheres to the inner papilla wall on one side. The interior of the penis sheath is covered by numerous small longitudinal folds. There are only 2 pairs of vaginal

plicae. At the base of the dart sac ducts they form well-developed lobes. The spermathecal duct is almost straight, ending in a small oval spermatheca that falls considerably short of the lower edge of the albumen gland.

#### Genus *Hygrohelicopsis* Shileyko, gen. nov.

The shell is very flattened, lilac-chestnut-colored, with pale transverse spots. The aperture is rather large, with the body whorl rapidly increasing in height. The umbilicus is narrow but deep, penetrating well into the shell. Unlike all other Trichiinae, in this genus, the right-hand ocular retractor does not cross the distal part of the genitalia, passing between the penis and vagina, but only runs beside them. A further distinguishing mark is the seeming absence of the inner pair of dart sacs, which, however, are present internally. The flagellum is about as long as the penis and the epiphallus. Inside the verge the seminal duct is surrounded by a pair of intrapapillar cavities embracing it from 2 sides.



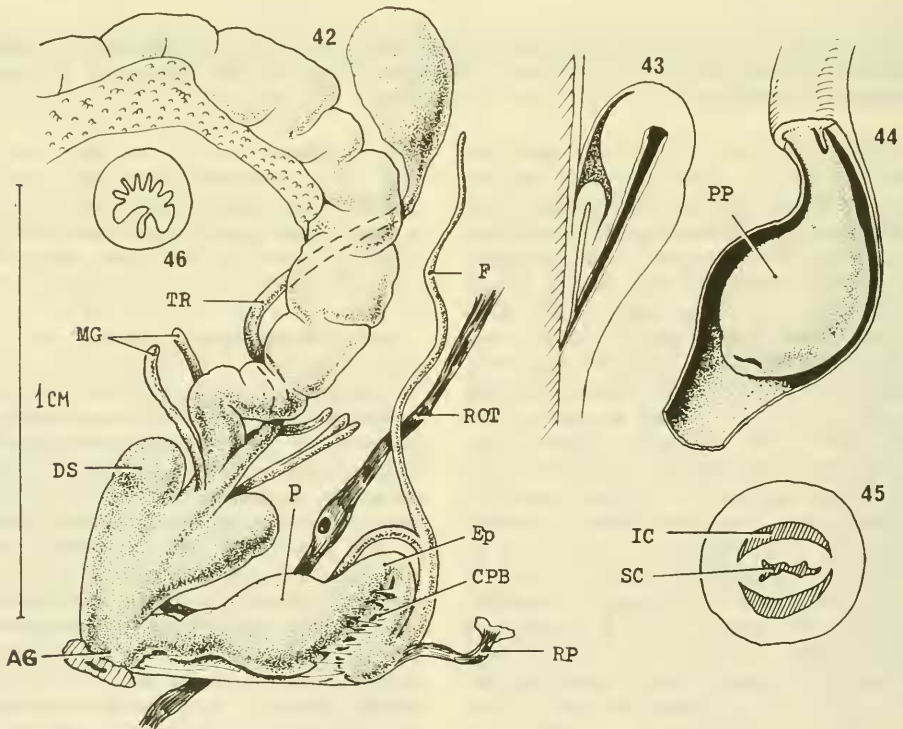
*Hygrohelicopsis darevskii* Shileyko, sp. nov.  
Figs. 42-46; Pl. III, 9

Two specimens were examined. They were collected in Chegem Valley, N slope of the central Caucasus, USSR, at 200-2500 m above sea level, on 9-10 August 1965, by I. S. Darevski and identified by me. Holotype and paratype are in the Zoological Institute, USSR Academy of Sciences, Leningrad.

The shell is very lowly conical, of a lilac-chestnut color, with pale, wide transverse spots and a silky gloss. It is sculptured with irregular, smooth, transverse wrinkles, particularly on the upper part of the body whorl; the basal part is smoother. In places there are weak spiral lines. The aperture is rather large, oblique and somewhat deflected. The aperture edges are simple, but the basal edge is slightly reflected. At the rim there is a heavy, snow-white lip which is seen through the body whorl wall as a wide,

white line with indistinct limits. During development not 1 lip alone but 2-3 lips are formed; earlier lips are also seen as wide, light lines. There are 5 whorls of moderately rapid growth. The body whorl increases rapidly in height so that the parietal wall of the aperture makes a rather acute angle with the periphery of the body whorl. This character easily distinguishes this species from *Caucasigena schaposchnikovi*, in which the lower part of the palatal aperture wall is almost parallel to the periphery of the body whorl (see Pl. III, 9a and Pl. V, 19a and 20a). The umbilicus is narrow but deep. The nuclear whorls are smooth, lightly horn-colored; they are vaguely separated from the definitive whorls. The dimensions are

|              | Holotype<br>(mm) | Paratype<br>(mm) |
|--------------|------------------|------------------|
| Shell height | 6.0              | 6.0              |
| Shell width  | 10.5             | 10.4             |



FIGS. 42-46. *Hygrohelicopsis darevskii* Shileyko, sp. nov., holotype, Chegem Valley, N slope of central Caucasus, USSR, 10 August 1965. 42, reproductive tract; 43, longitudinal section of dart sac region; 44, penis, penis sheath partly removed; 45, transverse section of verge showing paired intrapapillar cavities of crescent-shaped cross-section on either side of seminal duct, which is fused with the papillar wall at 2 opposite points; 46, cross-section of epiphallus.



Anatomically this species stands apart from other representatives of the *Trichia* s. lat. group. The oviduct makes a sudden bend. There are 4 mucous glands; 1 or 2 are 2-branched. The upper and lower vagina in the dart sac region is bulbous; the dart sacs are very large. Externally only 1 pair of dart sacs is seen (Fig. 42) but upon dissection one can see small rudimentary inner sacs fully covered by a common connective tissue sheath (Fig. 43). The flagellum is thin, about twice as long as the epiphallus. The epiphallus sharply curves twice and is held in this position by connective tissue bands. The penis is globose, inflated. The verge is cylindrical proximally and bulbous distally. The seminal duct is surrounded by a pair of intrapapillar cavities (Fig. 45). The penis sheath is smooth inside. The spermathecal duct is long, slightly curved, with a bulky rounded spermatheca almost reaching the albumen gland.

It is emphasized that the right-hand ocular retractor (ROT, Fig. 42) is situated as is characteristic for the "Helicellinae" auct.: i.e., it passes near the distal genitalia

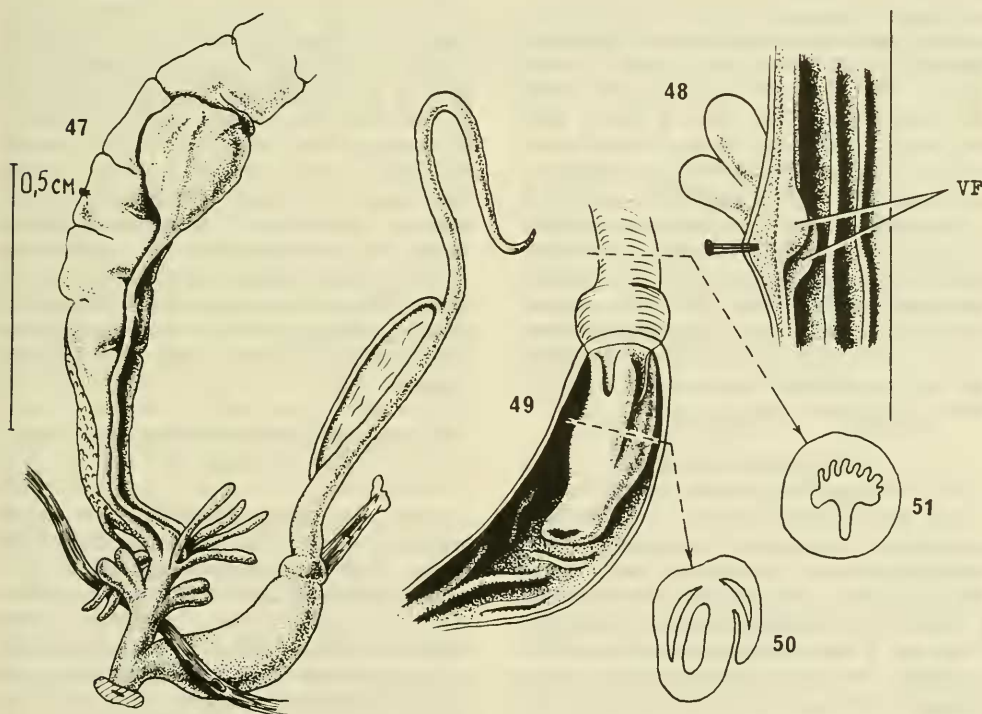
but not between them. We shall return to this point in the discussion.

#### Genus *Teberdinia* Shileyko, gen. nov.

The shell is brownish-yellow in color with a slightly inflated basal part; it is lowly conical with an umbilicus of medium size. The outer and inner dart sacs are closely apposed and fused along the greater part of their length, but the inner sacs are distinctly separate from the upper vagina. The seminal duct is surrounded by a pair of intrapapillar cavities. It is the only Caucasian form with a deep longitudinal groove on the surface of the penis papilla that separates off a lobe, and the only form so far observed in which one of the intrapapillar cavities reaches into the lobe. Genus monotypic.

#### *Teberdinia zolotarevi* (Lindholm, 1913) Figs. 47-51; Pl. III, 10

One specimen was examined anatomically. It was collected from the *Teberdia*



FIGS. 47-51. *Teberdinia zolotarevi* (Lindholm), Teberdia Nature Reserve, NW Caucasus, USSR, 24 July 1958. 47, reproductive tract; 48, inner structure of vagina in dart sac region; note lobes on vaginal folds; 49, penis, penis sheath partly removed; 50, cross-section of verge; 51, cross-section of epiphallus.

Nature Reserve, NW Caucasus, USSR, by L. Arens on 24 July 1958; I identified it. Holotype and paratype (not fully adult) are at the Zoological Institute, USSR Academy of Sciences.

The shell is lowly conical with a markedly bulbous basal part and flattened whorls. The color is brownish-yellow. It is sculptured with smooth radial wrinkles and spiral lines. The aperture is oblique, and in the basal (palatal) part it is twisted slightly to the right. The aperture edges are simple, slightly reflected. The columellar edge is more reflected. Near the edge there is a heavy white lip, visible through the shell as a wide, light line. The shell is perforate, and the aperture is slightly covered by the columellar edge. There are 5.75 whorls. The holotype shell height is 6.7 mm; width, 11.3 mm.

The oviduct forms a smooth bend. There are 3 mucous glands, each with 2 branches. The dart sacs are small, closely pressed together in pairs and directed away from the upper vagina. The lower vagina is short, and cylindrical, with narrow but rather high plicae. At the base of the dart sac duct they form rather round lobes. The flagellum is longer than the straight cylindrical epiphallus. Between the flagellum and the penis there is a clear-cut ring (bullae). Internally the penis sheath bears thin long plicae. The verge is short, bag-like, blunt at the edge. A deep longitudinal groove occupies about half the length of the verge. Of the 2 intrapapillar cavities, 1 is adjacent to the seminal duct and the other characteristically extends into the longitudinal lobe separated by the above-mentioned groove (Fig. 50). The spermathecal duct is very thin and closely pressed to the spermoviduct; it ends in a bulky, bag-like receptaculum seminis that does not reach the albumen gland.

**Genus *Kokotschashvilia***  
Hudec & Lezhawa, 1969

The shell is lowly conical to top-shaped, white or horny, perforate to umbilicate and perspective. It is sculptured with radial lines, spiral lines or granules. The flagellum is about half as long as the epiphallus. There are 4 mucous glands, each with 2-4 branches. The dart sacs are massive and rounded. The receptaculum seminis is very bulky; when it is not full its walls are collapsed, so in this condition it looks atypical. The seminal duct is surrounded

either by a pair of intrapapillar cavities or, when a longitudinal partition between the cavities is absent, by a single intrapapillar cavity with a crescent-shaped cross-section that embraces the seminal duct from 3 sides. The seminal duct may either adhere closely to the inner papilla wall on one side or on a thin, long band on that same side or also on the opposite side.

Type-species: *Helix holotricha* Boettger, 1884

***Kokotschashvilia makvalae***  
(Hudec & Lezhawa, 1969)  
Figs. 52-56

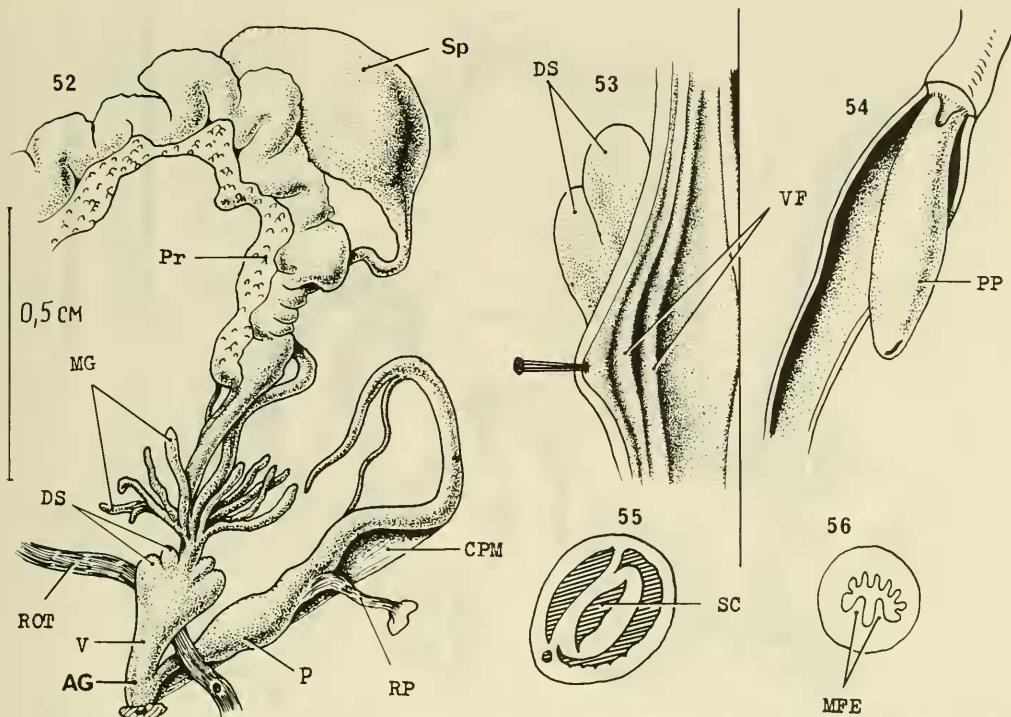
The anatomy of 1 specimen was studied. It was collected at Balda village, Gegechkor region, NW Georgia, Grusinian SSR, on 3 May 1967 by G. Lezhawa and identified by V. Hudec. A description of the shell is given by Hudec & Lezhawa (1969a, b).

The spermoviduct passes straight and without curving into the oviduct, which also shows no bend. Each of the 4 mucous glands has 2-3 branches. The inner dart sacs are slightly smaller than the outer ones. Inside the vagina there are, laterally, 2 pairs of long plicae. At the exit of the dart sac duct the vaginal plicae do not form any lobes. The flagellum is approximately half as long as the slightly curved epiphallus. A penial membrane, rather weakly developed, is present. The penis is fusiform, slightly bulbous. The penis sheath is smooth inside. The verge is fusiform. The seminal duct is held in place by 2 longitudinal bands. There is a fine channel in the papilla wall at the place of attachment of 1 of the bands. The spermathecal duct is moderately twisting, ending in a wide receptaculum seminis that almost reaches the albumen gland.

***Kokotschashvilia tanta* Shileyko, sp. nov.**  
Figs. 57-61; Pl. III, 11

Specimens were collected from alpine meadows near Lebarde village, Gegechkor region, NW Georgia, Grusinian SSR, on 5 July 1962 by M. G. Natsvlishvili and identified by me. Three specimens were examined anatomically. The holotype and 6 paratypes (2 damaged) are at the Zoological Institute, USSR Academy of Sciences, Leningrad.

The shell is lowly conical to lowly top-shaped. Fresh shells are a light horn color.



FIGS. 52-56. *Kokotschashvilia makvalae* (Hudec and Lezhawa), Balda village, Gegechkor region, NW Georgia, Grusinian SSR, 3 May 1967. 52, reproductive tract; 53, inner structure of vagina in dart sac region; 54, penis, penis sheath partly removed; 55, transverse section of verge; the 2 stalks joining the seminal duct to the papillar wall are the longitudinal bands, in cross-section, which attach the duct to the papilla; 56, cross-section of epiphallus.

The color is darker above and under the periphery of the body whorl, forming vague darker lines. The shell is sculptured with irregular, rather fine radial lines; in places there are vague granulate and spiral lines, more clearly seen on the periphery and the basal part of the shell. A pale line runs above the suture. The aperture is roundly lunate, oblique and deflected. A narrow light spiral line starting a distance back of the aperture runs high on the shoulder of the whorl. The umbilicus is eccentric, and through it the penultimate whorl is fully visible. A pale line on the shell surface corresponds to the lip.

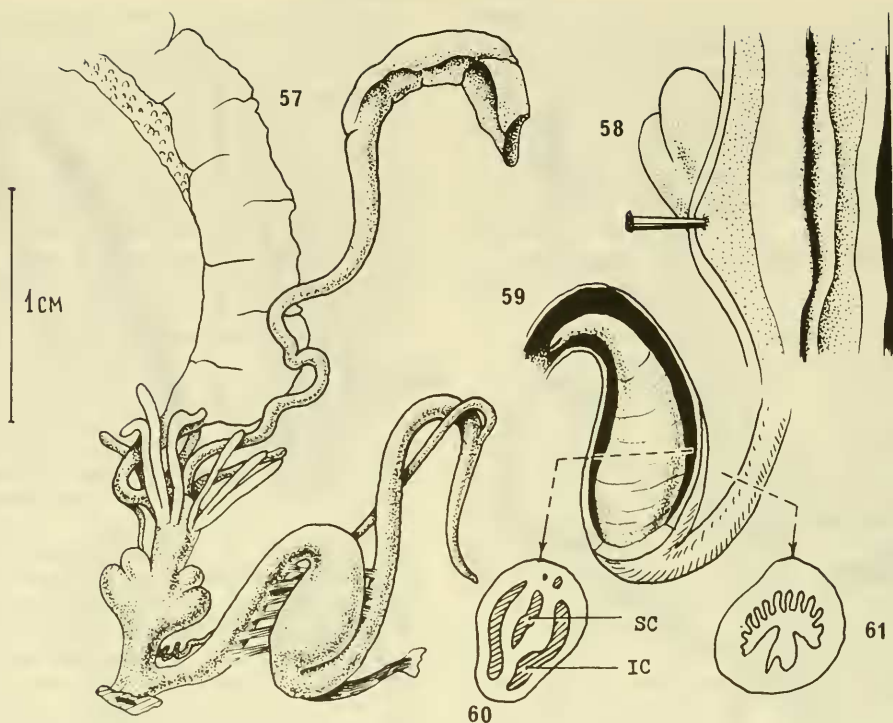
The shell is similar to that of *K. makvalae*, its nearest relative, but differs by its darker color (*K. makvalae* is uniformly white), by the presence of spiral sculpture, by a more oblique aperture, by a larger number of whorls (6.5-7.0 compared to 6) and by its definitely larger size. The largest of our specimens of *K. makvalae* has a

diameter of 21.5 mm compared to 22-27 mm in *K. tanta*. It differs from *K. eberhardi* in color and shape (*K. eberhardi* is yellowish and has a wider umbilicus and a higher spire) and by its much larger size. Shell measurements, including 5 of the paratypes, are as follows:

|              | Holotype<br>(mm) | Paratypes<br>(mm) |      |      |      |      |
|--------------|------------------|-------------------|------|------|------|------|
| Shell height | 16.8             | 16.7              | 18.0 | 14.6 | 16.3 | 17.8 |
| Shell width  | 25.5             | 27.0              | 24.7 | 22.2 | 25.0 | 26.3 |

More distinct interspecific differences are in the reproductive anatomy, particularly in the inner structure of the verge. The oviduct makes a smooth bend; it is thin but becomes wider below. There are 4 mucous glands, each with 2-3 branches. The dart sacs are rather massive, globose. The vaginal plicae are heavy and form wide lobes. The flagellum is about half the length of the epiphallus. The latter is





FIGS. 57-61. *Kokotschashvilia tanta* Shileyko, sp. nov., paratype, Lebarde village, Gegechkor region, NW Georgia, Grusinian SSR, 5 July 1962. 57, reproductive tract; 58, inner structure of vagina in dart sac region; 59, penis, penis sheath partly removed; 60, cross-section of verge; 61, cross-section of epiphallus.

attached to the penis by connective tissue bands. The penis consists of 2 parts: a globose fusiform proximal part and a cylindrical distal one; these are also connected by connective tissue bands (Fig. 57). The verge lies in the former. As in *K. makvalae*, the seminal duct is surrounded by a pair of intrapapillar cavities, but in this species one of the partitions separating the pair is practically absent; thus the seminal duct is closely united with the inner papilla wall on that side (cf. Figs. 55 and 60). As in *K. makvalae*, there is a narrow channel in the papillar wall along the seminal duct, and near it, moreover, a very fine capillary. The spermathecal duct is thin and slightly curving; it gradually merges with the bag-like receptaculum seminis (spermatheca), which was in a flaccid state in all specimens studied. The spermatheca was apparently empty because of the time of collection (June).

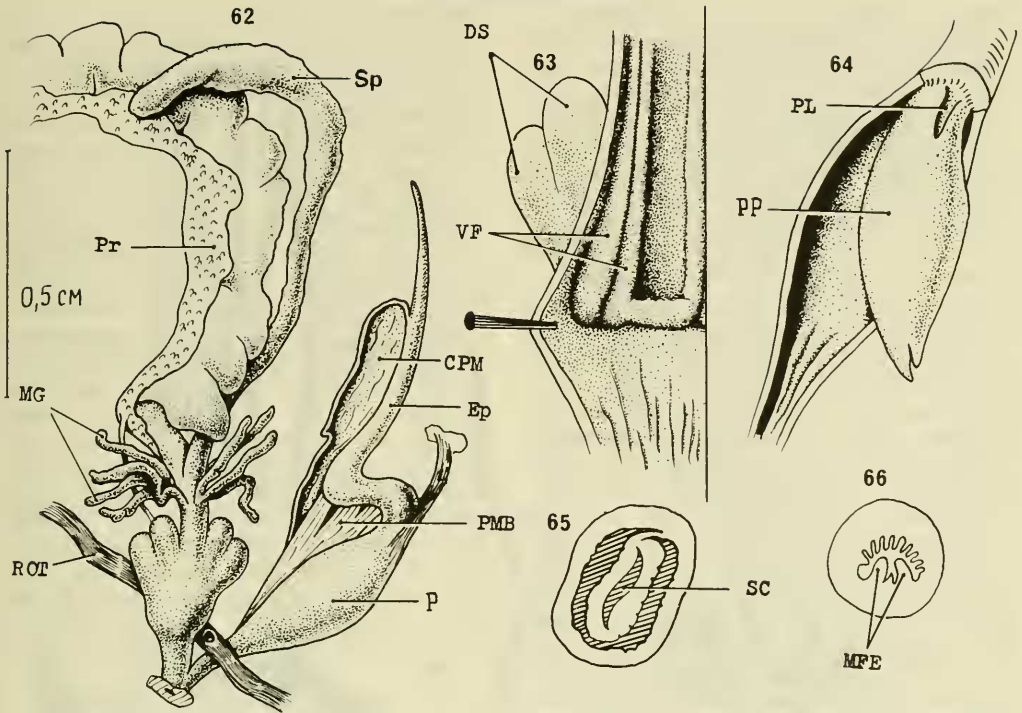
It is noteworthy that in *K. holotricha* and *K. eberhardi*, which were collected during June-July also, the spermathecas were empty, whereas in *K. makvalae* and

*K. phaeolaema*, collected in early and mid-May, it appeared to be full (cf. Figs. 52, 57, 62, 67 & 71).

#### *Kokotschashvilia holotricha* (Boettger, 1884) Figs. 62-66

Two specimens were examined. They were collected at Tsebelda village, near Sukhumi, in the Black Sea coastal region, Grusinian SSR by G. Lezhawa on 15 June 1968 and identified by V. Hudec. A good shell description is in Likharev & Rammelmeyer (1952).

The spermoviduct curves as it passes to the free oviduct, which itself is straight. There are 4 mucous glands, all with 2 branches. The dart sac region is set off from the lower part of the vagina, which is narrower. The vagina is short. Vaginal plicae occur in pairs and occupy a lateral position; they are abruptly cut off distally and connected by a transverse fold (Fig. 63); the lower part of the vagina and genital atrium is either smooth internally or has irregular fine wrinkles. The flagellum is



FIGS. 62-66. *Kokotschashvilia holotricha* (Boettger), Tsebelda village, near Sukhumi, Black Sea region of Georgia, Grusinian SSR, 15 June 1968. 62, reproductive tract; 63, inner structure of vagina in dart sac region; 64, penis, penis sheath partly removed; 65, cross-section of verge; 66, cross-section of epiphallus.

short and conically tapering. It measures about half the length of the epiphallus, which is S-shaped and supplied with particularly well-developed connective tissue bands containing muscle fascicles. The penis is fusiform and has longitudinal folds in the vicinity of the genital atrium. The verge is fusiform; the seminal duct is connected to the inner surface of the papilla wall by 1 single long band and surrounded on all sides by an intrapapillar cavity (Fig. 5); the papilla wall does not include any channels.

Hudec and Lezhawa (1969a, b) did not comment on the S-shaped bend of the epiphallus in this species. Hesse (1931) pointed out that not all the mucous glands have 2 branches; some may be simple.

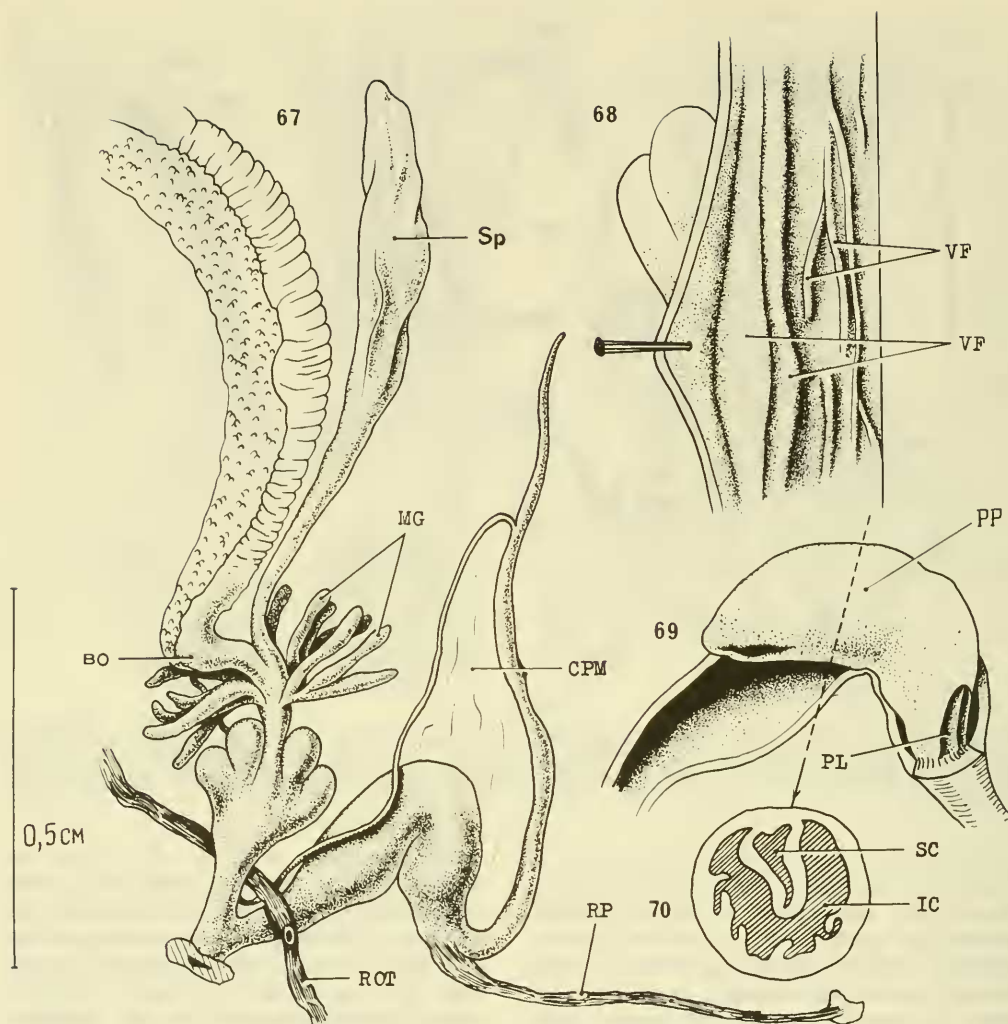
*Kokotschashvilia eberhardi*,  
Shileyko, sp. nov.  
Figs. 67-70; Pl. III, 12

Specimens were collected in July 1969 between the villages of Sioni and Kazbegi,

on the S slope of the central part of the main Caucasus range, Grusinian SSR, at an altitude of 2500-3000 m above sea level, by E. Clauss. They were identified by me. Four specimens were examined anatomically. The holotype and 4 of the paratypes are at the Zoological Institute, USSR Academy of Sciences, Leningrad.

The shell is compressedly conical to almost globose. Its coloration is characteristic: the background is a pale straw color that gradually becomes lighter near the sutures: above and under the periphery it may be darker, forming 2 dark bands. It has a sculpture of irregular radial wrinkles, more clearly expressed near the sutures. With a lens it can be seen that in fresh shells the wrinkles are lighter than the background, in fact almost white. There are granulose spiral lines, mostly on the basal part of the shell. The aperture is almost round; at its edge there is a well-developed white lip. This lip is clearly visible from the outside as a whitish-yellow band; 2-3 such lips are formed during the life of the





FIGS. 67-70. *Kokotschashvilia eberhardi* Shileyko, sp. nov., paratype, between Sioni and Kazbegi villages, S slope of central Caucasus, Grusinian SSR, July 1969. 67, reproductive tract; 68, inner structure of vagina in dart sac region; 69, penis, penis sheath partly removed; 70, cross-section of verge.

mollusk, and these earlier ones are also visible through the shell as light lines. The umbilicus, though narrow, is perspective. There are 6 whorls. The dimensions of our shells are:

|              | Holotype<br>(mm) | Paratypes<br>(mm) |      |      |      |      |
|--------------|------------------|-------------------|------|------|------|------|
| Shell height | 10.3             | 10.7              | 11.0 | 11.7 | 11.0 | 10.5 |
| Shell width  | 14.5             | 15.5              | 15.0 | 14.1 | 15.0 | 14.6 |

The shell of this species resembles that of *K. makvalae* and *K. tanta* in shape, though it differs in its smaller size, in color (*K. makvalae* is white and *K. tanta* horn-

colored) and also in sculpture. There are clearer distinctions yet in the structure of the reproductive organs.

The spermoviduct makes a sudden but smooth bend as it passes to the free oviduct, which itself is slightly bent. There are 4 mucous glands, each with 3-4 branches. The dart sacs are very massive and globose; the sac region is set off from the vagina by a slight narrowing of the lower vagina. In addition to the usual paired vaginal plicae in a lateral position, there are supplementary smaller vaginal plicae. Usually the basic plicae do not form lobes. The flagel-

lum is thin, and its length is about half that of the epiphallus, which is also thin, cylindrical and weakly curving. The penis is massive, more or less curved. There are no muscle bands, only a fine connective tissue membrane stretched among penis, epiphallus and vas deferens. The inner surface of the penis sheath is smooth. The verge is bulky and bag-like and has a large papillar lacuna. The seminal duct is closely fused to one side of the inner papillar wall and surrounded on all other sides by a wide intrapapillar cavity as in *K. tanta*; however, the inner papillar wall facing this cavity is not smooth, as in *K. tanta*, but bears many lamellae and folds (Fig. 70). The spermathecal duct is almost straight and demarcated from the receptaculum seminis, which has very thin walls. In the specimens studied the receptaculum walls were wrinkled and collapsed, the receptaculum apparently empty. The organ does not reach the albumen gland. The intense pigmentation of the pallial nerve is noteworthy.

**Kokotschashvilia phaeolaema**

(Boettger, 1886)

Figs. 71-76; Pl. IV, 13

Sixteen specimens were examined anatomically; 14 of these were collected on 14 May 1970 in Chegem Valley, which descends the N slope of the central Caucasus (USSR) as a tributary to the valley of the Terek; they were identified by me. Two specimens were collected from the Khunzah district of Daghestan on 26 August 1955 by T. Khasanov and identified by I. M. Likharev.

As this species is little known, the shell is described here. It is lowly conical and almost globose, light horny, yellowish or chestnut in color, with a diffuse light line at the periphery, radial folds and distinct spiral ridges. The aperture is roundly lunate, slightly deflected and oblique. The umbilicus is narrow and may be half-covered by the reflection of the columellar lip. There is a thick white lip on the inside edge of the aperture. During life the animal forms 3-5 such lips, which can be seen translucently as radial bands of a lighter hue. On the outside, closely joined to them, there is a line darker than the background of the shell. There are 6 whorls. The shell height (from 53 specimens) is 9-12 mm; the width, 10.5-16.0 mm.

Lindholm (1913) described *Helix (Fruticocampylaea) phaeolaema* Boettger var. *tenuitesta*, which differs by its small, thin-walled, translucent shell (height, 9-10 mm; width, 10.5-12 mm), with a translucent lip and a yellowish or light brown horny color. As these characteristics are all seen in some specimens of our series, it is not necessary to separate this form.

The oviduct makes a sudden sharp bend. There are 4 mucous glands, each usually with 2 branches, but sometimes we find a secondary branching in some particular gland. The dart sacs are well-developed and globose. The vaginal plicae are only moderately developed, but form clear-cut lobes near the opening of the dart sac duct. The length of the flagellum is 1/2 to 3/4 that of the epiphallus. The latter bends twice and is attached to the penis by a well-developed connective tissue membrane (CPM, Fig. 71) in which there are muscle bands. The penis is large, bag-like or globose. Its sheath is smooth inside, except that there are a few longitudinal folds near the genital atrium. The papilla is very inflated, globose or pear-shaped. The seminal duct is suspended from the papillar wall by 2 long bands; i.e., it is surrounded by a pair of intrapapillar cavities. In contrast to other species of this genus, the papillar walls are thick and contain additional intrapapillar cavities in the form of small scattered sinuses in the wall (Fig. 4), which therefore sometimes looks spongy. The receptaculum seminis is very massive and bag-like; its upper edge reaches the lower part of the albumen gland.

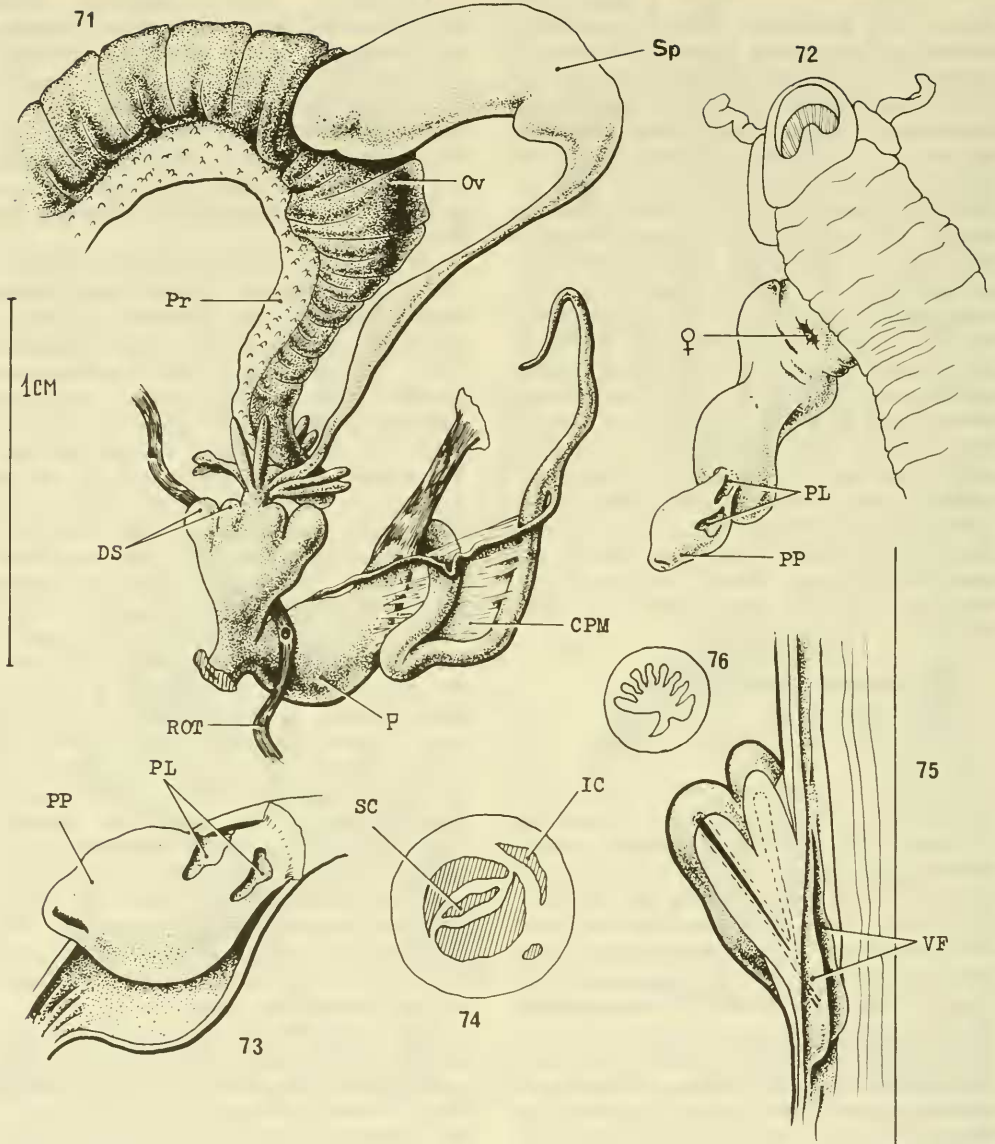
The characteristic peculiarity of this species is the intense pigmentation of the spermooviduct (especially on the oviduct side), of the distal part of the intestine, of the mesentery and of the surface of the circumesophageal nerve ring.

The gross morphology of the genitalia of this species was first described by Kalitina (1958: 159-160).

**Genus *Caucasigena* Lindholm, 1927**

The shell is almost flat to lowly conical, smooth or ribbed, umbilicate or perforate (subgen. *Dioscuria*). Inside the aperture edge there is a heavy white lip.

There are 3 or 4 mucous glands, each with 2 branches, and a tendency neither for secondary branchings nor for simple,



FIGS. 71-76. *Kokotschashvilia phaeolaema* (Boettger), Chegem Valley, N slope of central Caucasus, USSR, 14 May 1970. 71, reproductive tract; 72, penis in copulating position; verge (papilla) is moved out, penis sheath is turned inside out; 73, penis, penis sheath partly removed; 74, cross-section of verge; 75, inner structure of vagina in dart sac region; 76, cross-section of epiphallus.

nonbranching glands. Inside the papilla (verge) the seminal duct is very narrow. The longitudinal compartments of the intrapapillar cavity that lies on 1 side of the papilla are separated by longitudinal septa from one another and from the cavities (numbering from 3 to 9) that surround the seminal duct. The papillar lacunae are rather large.

Type-species: *Helix eichwaldi* L. Pfeiffer, 1846.

Subgenus *Caucasigena* s. str.

The shell is pale, with brown spiral bands that sometimes are so markedly developed they form nearly the whole background of the shell; in this case there



is a lighter line on the periphery. The radial sculpture varies from simple lines (ridges) to very rough ribs. The spiral sculpture appears either as fine striae or as very thin ribs. The flagellum is stout, conical, not more than 1/2 the length of the epiphallus, which is more or less straight. The inner dart sacs are the same size as the outer ones or slightly longer. The seminal duct is attached to the inner wall of the papilla by 1-3 long bands.

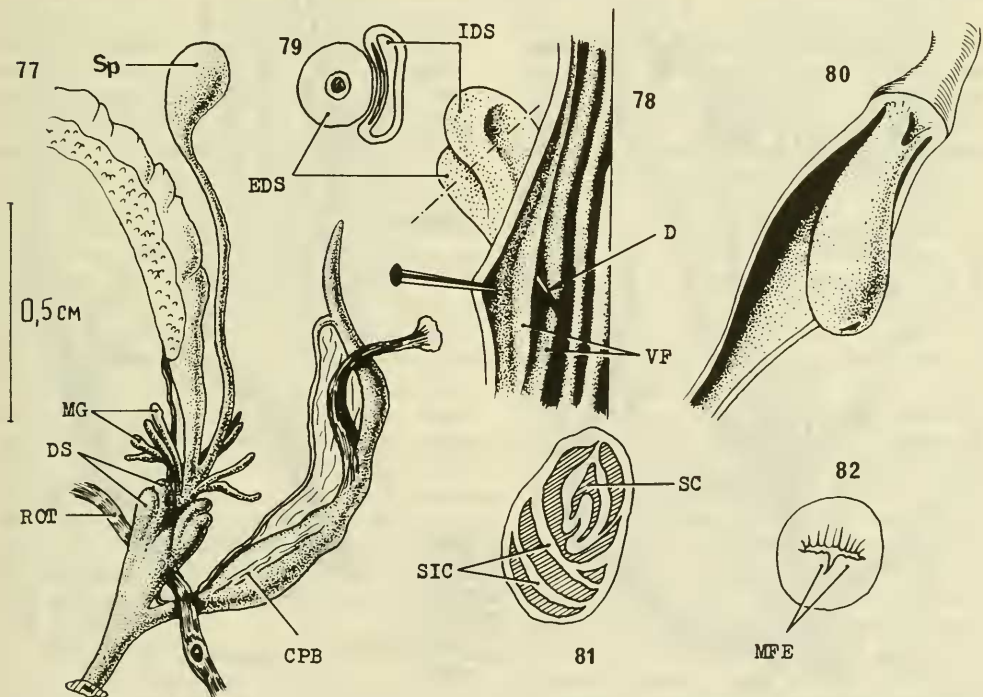
**Caucasigena (Caucasigena) armeniaca**  
(L. Pfeiffer, 1846)  
Figs. 77-82; Pl. IV, 14

The specimens described are from Mt. Bzovdal (Mt. Todar) in the Stepanavan region, Armenian SSR. They were collected on 18 July 1951 and identified by N. N. Akramovsky. Two of the 6 specimens available were dissected.

Because of some confusion in the literature, it is necessary to give a description of the shells. Records of this species in a number of districts of the main Caucasus

range are erroneous: all those from the N slopes of the Great Caucasus are referable to *C. rengarteni*, which Likharev & Rammelmeyer (1952) mistakenly placed in synonymy with *C. armeniaca* and omitted from their index.

The shell is lowly conical with a blunt angle at the periphery; it is relatively thick-walled, of a brownish horny color, with a light line at the periphery. The sculpture is very characteristic and consists of minute, smooth, radial ribs visible only under magnification and spiral periostracal ribs. At first sight they seem like the usual spiral lines, but when magnified 30-40 X and viewed with an oblique beam of light, they are clearly seen to be fine, sparsely but regularly spaced ribs; next to these are fine, rare, weakly curved hairs. The umbilicus is at first wide, funnel-shaped, but it then sharply narrows though it remains perspective. The aperture is roughly lunate, very oblique; on the inner rim there is a somewhat thickened yellowish lip. The shell has 5 gradually increasing whorls. The dimensions of the 6 specimens are:



FIGS. 77-82. *Caucasigena (Caucasigena) armeniaca* (L. Pfeiffer), Mt. Bzovdal (Mt. Todar), Stepanavan region, Armenian SSR, 18 July 1951. 77, reproductive tract; 78, inner structure of vagina in dart sac region; 79, cross-section of dart sacs; 80, penis, penis sheath partly removed; 81, cross-section of verge; 82, cross-section of epiphallus.

|                   |     |     |     |     |     |     |
|-------------------|-----|-----|-----|-----|-----|-----|
| Shell height (mm) | 4.0 | 4.0 | 4.3 | 4.5 | 3.7 | 5.0 |
| Shell width (mm)  | 7.9 | 8.0 | 8.0 | 8.5 | 6.7 | 8.7 |

The oviduct is short and straight. There are 4 mucous glands with 2 branches. The dart sacs are characteristic: the upper edges of the inner sacs pass beyond and curve over the elongate outer sacs, and their central portion curves medially (Fig. 77), sometimes almost bent over double. The inner pair of dart sacs is compressed from both sides (Fig. 79). The flagellum and epiphallus are both short; the former is thick and conical and about half as long as the latter, which is cylindrical and weakly curved. The penis is slightly bulbous, fusiform. On the surface of the penis sheath there are slight connective tissue bands (CPB, Fig. 77). Between vas deferens, epiphallus and penis is stretched a fine transparent connective tissue membrane (CPM). The interior of the penis sheath is smooth. The verge is club-shaped or fusiform, with

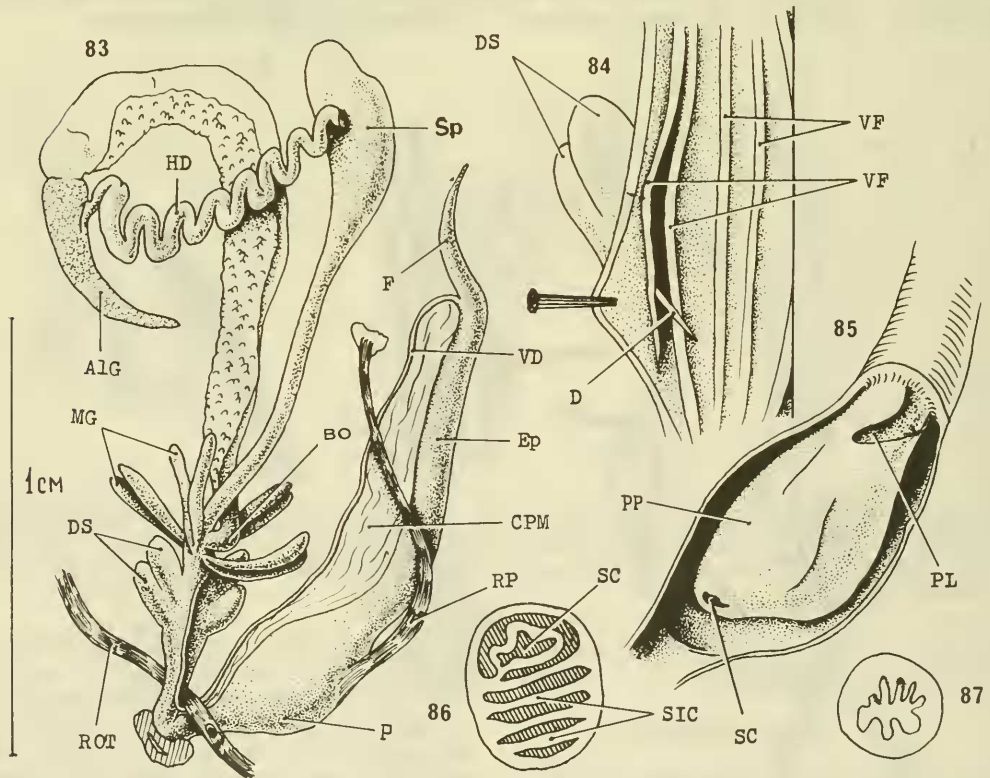
a well-developed papillar lacuna. The seminal duct is attached to the internal papillar wall by 2 long bands; further longitudinal septa divide off another 2-3 cavities (Fig. 81), making a total of 4-5 cavities. The spermathecal duct is almost straight and fine; the spermatheca is small and rounded; it nearly reaches the albumen gland.

*Caucasigena (Caucasigena) tshetschenica*  
(Retowski, 1914)

Figs. 83-87; Pl. IV, 15

Six specimens were dissected. I collected them on a limestone cliff in Kurtatin Valley at about the middle course of Phiagdon River, central part of the N Caucasus, USSR, on 19 September 1970, and I identified them.

The species was described by Retowski (1914) on the basis of 2 specimens collected by Köhnig on Mt. Bonoz-Mta in the Checheno-Ingush ("Chechnya"). Since the



FIGS. 83-87. *Caucasigena (Caucasigena) tshetschenica* (Retowski), Kurtatin Valley, middle course of Phiagdon River, central part of N Caucasus, USSR, 19 September 1970. 83, reproductive tract; 84, inner structure of vagina in dart sac region; 85, penis, penis sheath partly removed; 86, cross-section of verge; 87, cross-section of epiphallus.



species is little known, I here repeat its description, supplemented by my own observations.

The shell is small with a rather wide umbilicus, about 1/5 the shell width. The shell shape is almost flat to compressed conical. The color, as a rule, is horny with a pale line on the periphery accompanied by dark horn-colored bands on both sides. There are 5 relatively prominent, slowly increasing whorls, irregularly and roughly ribbed, with fine spiral lines in the spaces among the ribs. The ribs are white. The last whorl is angled or keeled. The aperture is strongly oblique, rounded, with a heavy white lip inside it. The parietal edge of the aperture is short. The columellar edge is widened and slightly reflected. The range of shell measurements from 100 shells is as follows: shell height, 3.2-4.8 mm; width, 6.5-9.8 mm.

Retowski gives the following sizes for his shells:

Shell height (mm) 4-4.5  
Shell width (mm) 7.7-8

The oviduct forms a rather smooth bend. There are 4 mucous glands, each with 2 branches. The dart sacs are elongate, and the rather large inner pair points distinctly away from the upper vagina; the outer pair are almost the same size. The flagellum is conical, stout, about half as long as the epiphallus. The penis is fusiform, globose. The male ducts are linked by a fine translucent connective tissue membrane (CPM, Fig. 83). The verge is relatively very massive and bag-like. The seminal duct is attached to the internal papillar wall by only 1 longitudinal band; i.e., it is surrounded by 1 encircling cavity on 1 side of the papilla. In the remaining part of the verge, longitudinal septa standing transversely divide the intrapapillar cavity into 3-5 parts (Fig. 86). The inside of the penis sheath is smooth, with vague partitions in its distal part. The spermathecal duct shows no curves; it ends in an elongate-oval receptaculum seminis, which does not reach the albumen gland.

*Caucasigena (Caucasigena) rengarteni*  
(Lindholm, 1913)  
Figs. 88-91; Pl. IV, 16; Pl. V, 17

Twenty specimens were dissected. These were collected in the central part of the N

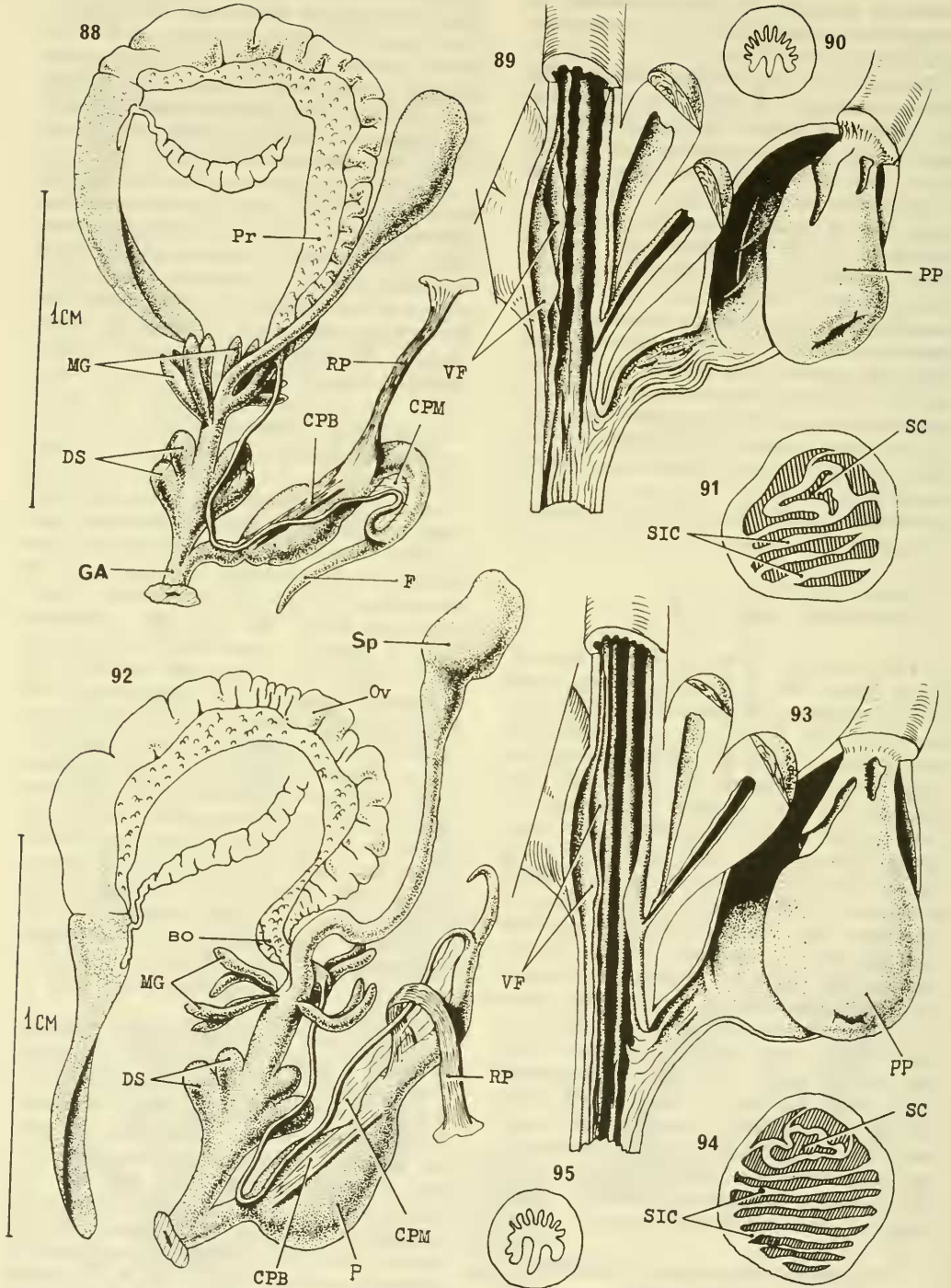
Caucasus (USSR) as follows: 10 specimens from the middle course of the Chegem River near Khushtosyr village, on 14 May 1970; 6 from the upper Chegem near Chegem village, on 19 May 1970; 4 from the old settlement of Ara-Boran between the Chegem and Baksan valleys, on 17 May 1970. These were all identified by me.

The shell characters are well given by Lindholm (1913), but he described the species from 3 specimens, whereas we had about 150 shells. It might now be added that some specimens have rare, wiry, short hairs on the surface of the shell. The dimensions may also be defined more exactly (Lindholm's values were 7 and 14.5 mm, respectively).

Shell height (mm) 5.8- 8.2  
Shell width (mm) 7.3-15.5

In the same article Lindholm described *Helix (Fruticocampylaea) gerassimovi* and outlined the differences between that species and *Helix rengarteni*, but from his description it is not quite clear what characters other than size can distinguish these 2 species. I was able to familiarize myself with the type-series of both of Lindholm's species (i.e., *gerassimovi* and *rengarteni*) and found that the differences between them depended on intrapopulational variability. Most of the specimens from Ara-Boran correspond to the diagnosis of *H. gerassimovi*, whereas in most of the series of *C. rengarteni* from the Chegem Valley one could see continuous gradations among the shells that invalidated the diagnosis of 2 separate species. Thus *H. gerassimovi* is a synonym of *Caucasigena rengarteni*. On Plates IV and V, shell 16 is typical for "*Helix*" *rengarteni* and shell 17 for *H. gerassimovi*.

The oviduct is almost straight. There are 4 mucous glands, each with 2 branches. The flagellum is thick, pointed and 1/2 to 3/4 the length of the epiphallus. The latter is straight or curved; it is connected with the penis by a very fine translucent connective tissue membrane (CPM, Fig. 88). On the surface of the penis sheath there are connective tissue bands including muscle fibers. The penis consists of a fusiform, globose proximal part, in which the papilla is located, and a slightly curved cylindrical distal part. The proximal part is smooth inside, with only small wrinkles or folds; the distal part bears many long wrinkles



FIGS. 88-91. *Caucasigena (Caucasigena) rengarteni* (Lindholm), Khushtosyrt village, Chegem Valley, central part of N Caucasus, USSR, 14 May 1970. 88, reproductive tract; 89, distal part of genitalia, dissected; 90, cross-section of epiphallus; 91, cross-section of verge.

FIGS. 92-95. *Caucasigena (Caucasigena) eichwaldi* (L. Pfeiffer), Chmi village, Darial valley, near Ordjonikidze (North Osetia), central part of N Caucasus, USSR, 8 May 1970. 92, reproductive tract; 93, distal part of genitalia, dissected; 94, cross-section of verge; 95, cross-section of epiphallus.

that merge with the folds in the genital atrium (Fig. 89). There are raised, rather heavy, vaginal plicae that form clear lobes at the mouth of the dart sac ducts. The verge is bulky and bag-like with a foramen in the shape of a wide slit and with large papillar lacunae. The seminal duct is held in place by 3 or 2 longitudinal bands; the intrapapillar cavity in the other half of the papilla is divided into 4-6 compartments by longitudinal septa. The spermathecal duct is straight or very weakly curved; the oval receptaculum seminis lies some distance away from the albumen gland (Fig. 88). For diagnostic characters, see below under *C. eichwaldi*.

**Caucasigena (Caucasigena) eichwaldi**  
(L. Pfeiffer, 1846)  
Figs. 92-95; Pl. V, 18

Nineteen specimens were dissected. I collected them in the Darial Valley, central part of the N Caucasus (USSR), near Ordjonikidze (North Osetia) as follows: 10 specimens near Kazbegi village, on 9 May 1970; 9 near Chmi village on 8 May 1970. The identification is mine.

A good shell description is given by Likharev & Rammelmeyer (1952). I nevertheless wish to point out that, although the shell of this species is rather variable as regards color, dimensions and particularly height of whorl, a keel is never found, nor any inclination toward forming an angle at the periphery, a character that distinguishes *C. eichwaldi* from *C. rengarteni*.

As the spermoviduct passes to the oviduct there is a rather sharp curve. There are 4 mucous glands, all with 2 branches. The dart sacs are massive, slightly elongate or globose. The inner vaginal structure is the same as in *C. rengarteni*. The flagellum length is at most half that of the epiphallus. The epiphallus does not make any sudden curve. The connective tissue membrane and penial band are as in *C. rengarteni*. The penis sheath also consists of 2 parts. The verge is massive. In it, the seminal duct is fixed in place by 3 longitudinal bands; i.e., it is surrounded by 3 intrapapillar cavities. The cavity in the remainder of the papilla is divided into 6-9 parts by parallel, transversely arranged, longitudinal septa (Fig. 94). The spermathecal duct forms a marked curve at its base. The receptaculum seminis reaches the lower edge of the albumen gland.

Differential diagnosis of  
***C. rengarteni* and *C. eichwaldi***

The anatomical distinctions between these 2 similar species can now be formulated. In *C. rengarteni* the mucous glands lie approximately at the level of the upper edges of the dart sacs; the uterus is straight; the spermathecal duct is almost straight; the flagellum length is not less, but usually a little more, than half the epiphallus length. The intrapapillar cavity is divided into 4-6 portions. In the type-species, *C. eichwaldi*, the mucous glands lie considerably above the level of the upper edges of the sacs. The uterus is bent and so is the spermathecal duct. The flagellum length is usually less than half that of the epiphallus. The intrapapillar cavity is divided into 6-9 parts.

**Subgenus Anoplitella Lindholm, 1929**

The shell is a light color with lilac spots, lines or marks; usually there are 2 or more less developed brown lines above and under the periphery of the body whorl. If these lines are well developed, the pale purple spots are absent. The shell is thick-walled, with a silky gloss. The umbilicus is more or less perspective. The flagellum is long and thin, a little longer than the curved epiphallus. The spermathecal duct is also long, thin and curved. The seminal duct is fused to the papilla on one side.

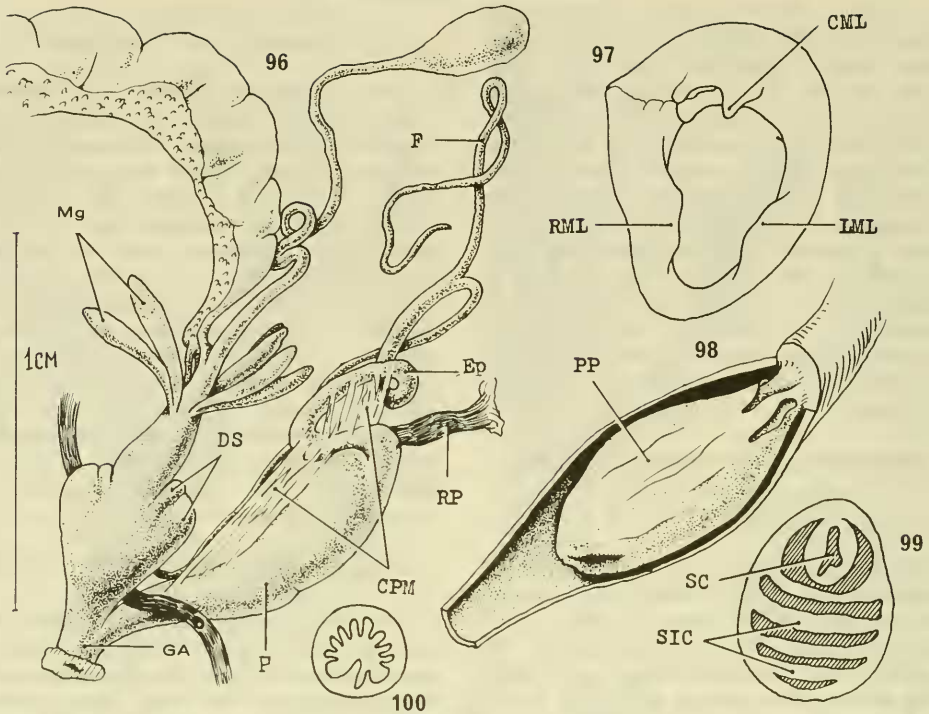
**Subgenus monotypic.**

**Caucasigena (Anoplitella) schaposchnikovi**  
(Rosen, 1911)  
Figs. 96-100; Pl. V, 19, 20

Seventeen specimens were dissected. I collected these in the central part of the N Caucasus (USSR) as follows: 10 specimens from the old Ara-Boran settlement between the Chegem and Baksan valleys, on 17 May 1971, and 7 from Chegem Valley near Khushtosyr village, on 15 May 1970. I identified them.

The shell is flattened, sometimes almost completely flat, smoothly rounded along the periphery and glossy. The umbilicus is rather narrow but perspective: all the previous whorls are visible through it. A little back of the aperture edge there is a thick white lip. The adult has 2-4 earlier lips that are visible through the whorls concerned as light radial lines. The shell is





FIGS. 96-100. *Caucasicigena (Anoplitella) schaposchnikovi* (Rosen), Khushotosyrt village, Chegem Valley, central part of N Caucasus, USSR, 15 May 1970. 96, reproductive tract; 97, mantle collar; 98, penis, penis sheath partly removed; 99, cross-section of verge; 100, cross-section of epiphallus.

sculptured with fine, irregular, radial striae and in places rare spiral lines. There are 6 whorls.

The dimensions, measured from 65 shells, were as follows:

Shell height (mm) 5.0- 8.5

Shell width (mm) 11.0-15.5

The original description was made from smaller specimens; the shell height was up to 6.5 mm and the width up to 10.5 mm.

In my collection the species is represented by 2 ecological forms that differ in the color and pattern of the shell and that do not occur together. These forms cannot be distinguished by other conchological characters, nor are there any anatomical distinctions. In shady valleys, in which insolation is slight, one finds the form with 2 distinct spiral brown bands of about equal width, 1 of which runs above and the other below the periphery. The distance between them is approximately equal to the width of each band. The upper band is visible along all whorls (Pl.

V, 20). In places with intense insolation (e.g., the old settlement of Ara-Boran) the shell color is chestnut to almost lilac; on this background there are more or less numerous bluish-white irregular lines and spots. In some places these spots coalesce into a larger patch or they form a reticulate pattern (Pl. V, 19). At the same time, in most specimens belonging to this second form, there are more or less developed spiral bands that are also characteristic for it. As is evident from study of his material at the Zoological Institute, USSR Academy of Sciences, Lindholm (1929) was dealing with such specimens when he described var. *balkariensis*.

The oviduct is almost straight but may be slightly curved. There are 3 or 4 mucous glands, each with 2 branches. The oviduct and upper vagina gradually increase in bulk from the upper to the lower part, being rather inflated in the region of the dart sacs. The outer sacs are large; the inner sacs are considerably smaller and fused with the upper vagina and the outer sacs. The flagellum is thin, slightly longer than the



epiphallus or equal to it, and coiling. The epiphallus is more or less coiled. There are well-developed connective tissue bands stretched between parts of the epiphallus and between the distal epiphallus and the distal penis. The penis is massive, elongate and smooth on the inside. The verge is sac-like with an opening forming a wide slot and with well-developed lacunae. The seminal duct adheres to the papillar wall on 1 side; the papillar cavity is subdivided into 4-6 parts (Fig. 99). The spermathecal duct is long, thin and coiled. The receptaculum seminis is small and oval; it reaches the albumen gland.

Subgenus *Dioscuria* Lindholm, 1927

The shell is thin-walled, brittle, with a silky gloss and a large aperture; depressed, conical. The umbilicus is very narrow and almost completely covered by the reflection of the columellar edge. The length of the flagellum is about half that of the epiphallus. The seminal duct is not separated from the papillar wall.

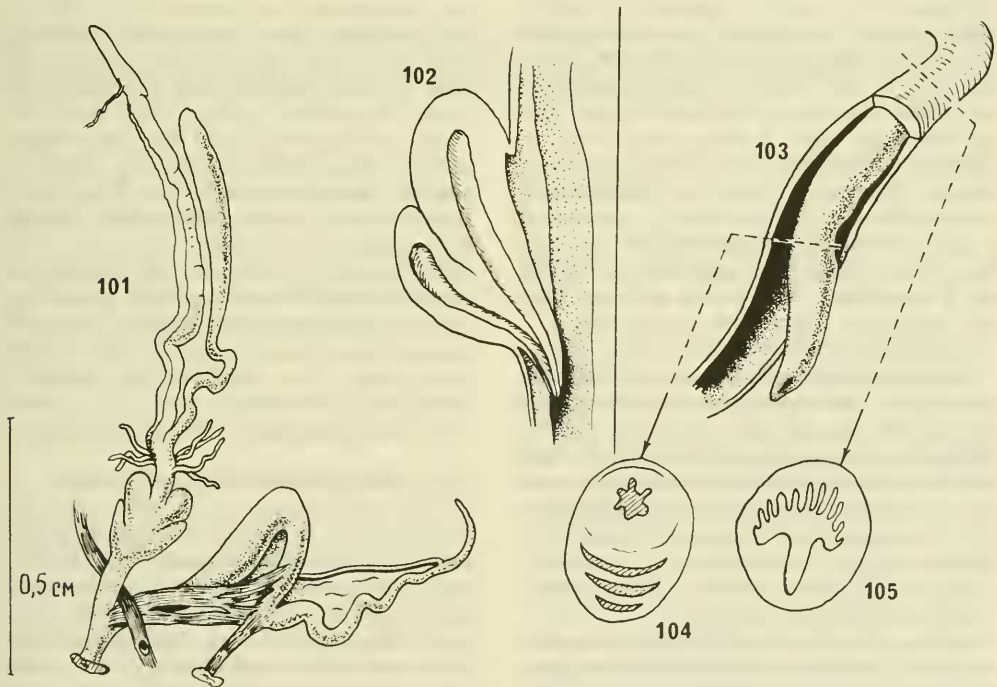
Subgenus monotypic.

*Caucasigena (Dioscuria) thalestris*  
(Lindholm, 1927)

Figs. 101-105; Pl. VI, 22

One not fully mature specimen was dissected. It was collected from Novy Aphon (New Athos), N of Sukhumi, Black Sea region of Georgia, Grusiniian SSR, on 2 July 1913, by Nasonov, and identified by Likharev. A shell description is given by Likharev & Rammelmeyer (1952).

The oviduct forms a slight bend. There are 3 mucous glands, each with 2-3 branches. These are situated slightly higher than the dart sacs. The inner dart sacs are a little larger than the outer ones. The vaginal plicae do not form lobes but are relatively well developed. The flagellum is about half the length of the epiphallus, which is wavy and curving. The penis forms 1 U-bend. A heavy muscle band between penis and epiphallus consists of several anastomosing strands. The verge is long and cylindrical. The seminal duct runs in the thickness of the papillar wall. The intrapapillar cavity lying in the wall on 1 side of the verge is divided into 3 parallel



FIGS. 101-105. *Caucasigena (Dioscuria) thalestris* (Lindholm), Novy Aphon, N of Sukhumi, Black Sea region of Georgia, Grusiniian SSR, 2 July 1913. Specimen not fully mature. 101, reproductive tract; 102, inner structure of vagina in dart sac region, 103, penis, penis sheath partly removed; 104, transverse section of verge; broken circle indicates boundary between external and internal layers of papillar tissue; 105, cross-section of epiphallus.

transverse compartments by longitudinal septa (Fig. 104). The spermathecal duct is tortuous. The elongated receptaculum seminis does not quite reach the albumen gland.

My data differ somewhat from those of Hesse (1931). According to his illustrations, the flagellum is slightly longer than the epiphallus; there is no indication of any penial muscle bands, and the spermathecal duct is short. Unfortunately not all Hesse's drawings are accurate, as he generally ignored muscle and connective tissue attachments. On the other hand, it should be kept in mind that I have examined only 1 not fully adult specimen, and such a character as flagellum length may be influenced by age variation. The same applies to the length and shape of the spermathecal duct.

#### Genus *Plicuteria* Shileyko, gen. nov.

The shell is depressedly conical with a sharp apex, covered with radial lines, yellowish-white, rarely hirsute; the suture is deep. The lip of the aperture is not thickened but weakly developed. Vaginal plicae appear each as a row of prismatic lamellae of equal size. The conical flagellum is half the length of the epiphallus or less. The epiphallus is almost straight. The spermathecal duct is very short. The receptaculum seminis is irregularly pear-shaped. The verge bears on its surface 2 longitudinal diametrically positioned grooves. In its distal part the seminal duct hangs from the inner walls of the papilla on 2 long bands, and in the proximal part it is fused to 1 side of the papillar wall.

Genus monotypic.

It is not clear why Polinski (1924) did not single out this snail as a separate species or subspecies. According to his illustrations and description, he took into account features of the outer genitalia such as the sturdy flagellum, spermathecal duct and receptaculum seminis, which are distinct enough to separate it from other European *Trichia*. The shell of this snail is evidently distinctive also.

At any rate, the new genus is unique in that the longitudinal vaginal plicae are subdivided by regular transverse prismatic folds that form a dense pattern on the internal wall of the vagina, and the spermathecal duct is shorter than in any other form of this group.

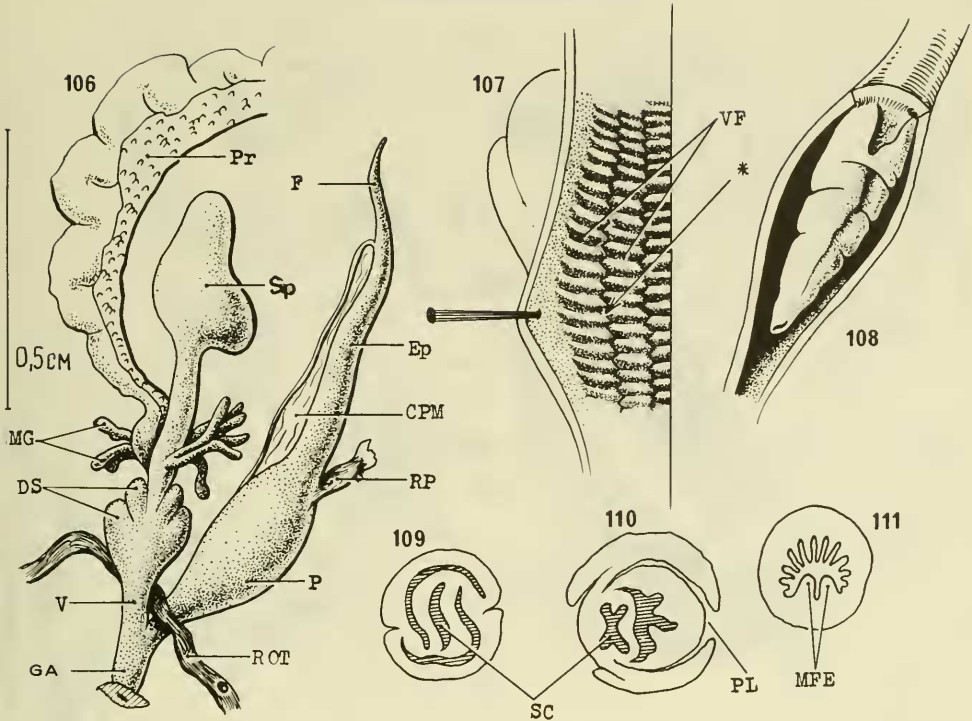
#### *Plicuteria lubomirski* (Slóssarski, 1881) Figs. 106-111; Pl. VI, 23

One specimen was examined. It was collected near the town of Olomouc, Moravia, Czechoslovakia, on 16 April 1964 and identified by V. A. Hudec.

As it emerges from the spermoviduct, the oviduct forms a definite bend. There are 4 mucous glands, each with 2-3 branches. The outer dart sacs are somewhat more massive than the inner ones, whose upper tips reach well beyond those of the outer sacs. The lower vagina is rather long and cylindrical. Its inner structure is most characteristic and unlike that of any other species; the vaginal plicae are clearly divided into regular rows of prismatic lamellae (Fig. 107). The male duct is elongate, neither curving nor twisted. The length of the conical flagellum is less than that of the thick, cylindrical epiphallus, which is connected to the vas deferens by a very fine membrane. The penis is fusiform; the penis sheath is smooth inside. The verge bears 2 shallow longitudinal furrows on its surface (Figs. 108, 109), as well as a few incomplete ring grooves (Fig. 108). In the proximal part of the verge the seminal duct is adjacent to the papillar wall on one side. On the opposite side it borders on a large intrapapillar cavity. Deep folds here reach into the verge wall from the papillar lacunae (Fig. 110). Distally (Fig. 109), the seminal duct lies encircled by 2 cavities of sickle-shaped cross-section. Their position, in conjunction with the thickness of the wall, supports the idea that cavities are thus formed during ontogenesis, most likely in the thickness of the papillar walls. The spermathecal duct is very thick, straight and short. The receptaculum seminis is irregularly pear-shaped and quite distant from the lower edge of the albumen gland.

#### Genus *Trichia* Hartmann, 1840

The shell is low to depressed conical, rather brittle, of a brownish horn color, with a more or less narrow umbilicus. As a rule there are hairs on the shell surface, which are absent in the adult specimens of some species. A thickened lip is either absent or occupies the basal edge of the aperture. There are 4 mucous glands, usually with 2 branches each. The dart sacs are elongate and more or less club-shaped. Inside the verge the seminal duct is en-



FIGS. 106-111. *Plicuteria lubomirskii* (Słóssarski), Olomouc, Moravia, Czechoslovakia, 16 April 1964. **106**, reproductive tract; **107**, inner structure of vagina in dart sac region; \*stylophore opening; note that longitudinal folds have become rows of prismatic lamellae; **108**, penis, penis sheath partly removed; **109**, **110**, cross-sections of verge at different levels; **111**, cross-section of epiphallus.

circled by a pair of intrapapillar cavities. There may be 1 further narrow slit-like cavity in the papillar wall.

The type-species is *Helix hispida* Linné. It was formerly thought to be *T. filicina* L. Pfeiffer, but Forcart (1958) proved that Hartmann, when he determined the genus *Trichia* with *T. filicina* as the type-species, really meant *T. hispida*.

#### Subgenus *Petasina* Beck, 1847

The shell is dome-like, with fine short hairs and a very narrow umbilicus. On its basal edge the lip sometimes bears a heavy swelling. The 4 mucous glands are simple, not branched, and some of them are only partly divided into 2. The inner pair of dart sacs is quite separate from the outer pair as well as from the upper vagina: the upper tips of the inner sacs reach well beyond the place of attachment of the mucous glands. The receptaculum seminis is very bulky and of a characteristic hammer shape.

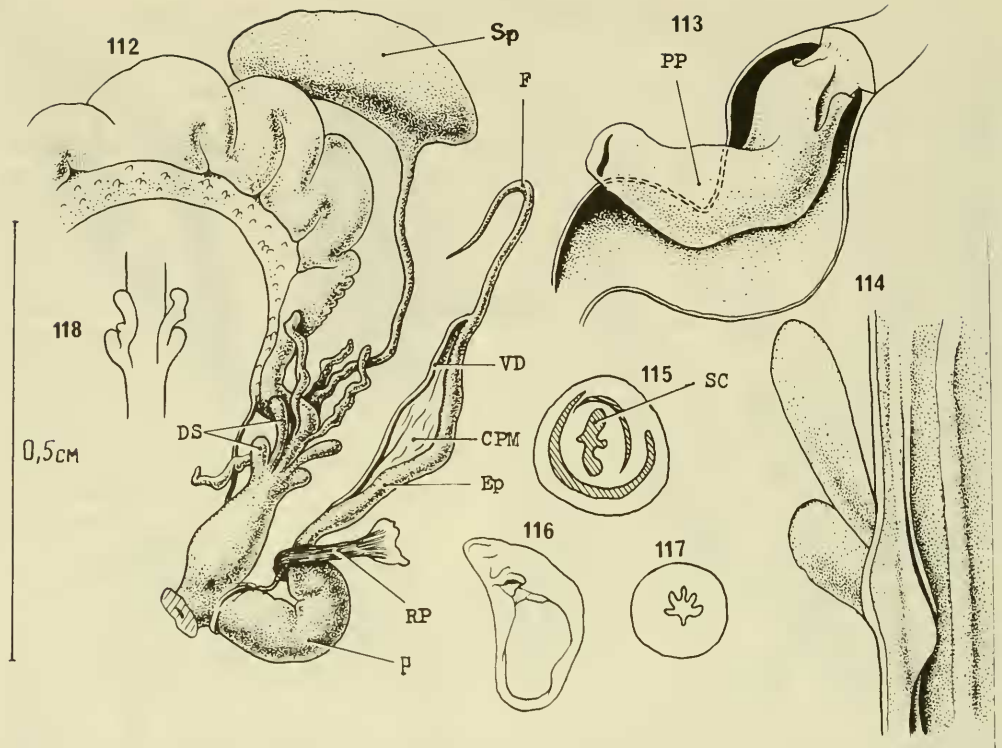
Type-species: *Helix unidentata* Draparnaud, 1805.

#### *Trichia* (*Petasina*) *unidentata* (Draparnaud, 1805)

Figs. 112-118; Pl. VI, 24

Five specimens were examined anatomically: 2 from central Czechia, Czechoslovakia, collected on 8 September 1969 by J. Buchar and identified by myself, and 3 from the High Tatra Mountains, Slovakia, Czechoslovakia, collected on 20 July 1964 by V. Hudec and identified by him.

As the spermoviduct passes into the oviduct, it curves weakly; the free oviduct itself is also slightly bent. There are 4 mostly unbranched, somewhat kinky mucous glands. The inner dart sacs are long, well separated, club-shaped; the outer ones are considerably shorter. One of the specimens had a distinct knobby thickening on the inner sacs (Fig. 114). The lower vagina is inflated and fusiform. The vaginal plicae are weakly developed, but there



FIGS. 112-118. *Trichia (Petasina) unidentata* (Draparnaud), central Czechia, Czechoslovakia, 8 September 1969. 112, reproductive tract; 113, penis, penis sheath partly removed; 114, inner structure of vagina in dart sac region; 115, cross-section of verge; 116, mantle collar; 117, cross-section of epiphallus; 118, dart sacs of another specimen from same location.

are distinct lobes at the openings of the dart sac ducts. The flagellum is about 2/3 the length of the cylindrical, almost straight epiphallus. The membrane connecting the distal parts of the male duct is very fine and translucent. The penis is cylindrical, straight or curved. The seminal duct is attached to the papillar wall by 3 longitudinal bands and surrounded by a pair of intrapapillar cavities with a crescent-shaped cross-section. The spermathecal duct is fine and slightly wavy; it does not join the massive receptaculum seminis apically but from below (hammerhead shape). It is of interest that in specimens collected in July and September the spermatheca was full.

#### Subgenus *Trichia* s. str.

The shell is flattened; the contour of the whorls is not dome-like but conical. The umbilicus is wider than in representatives of the subgenus *Petasina*. The inner dart sacs are not so sharply separated. There are 4 mucous glands, each with 2 branches; in

some glands the second branch is reduced. The mucous glands are attached considerably above the tips of the inner dart sacs. The receptaculum seminis is oval and rather small.

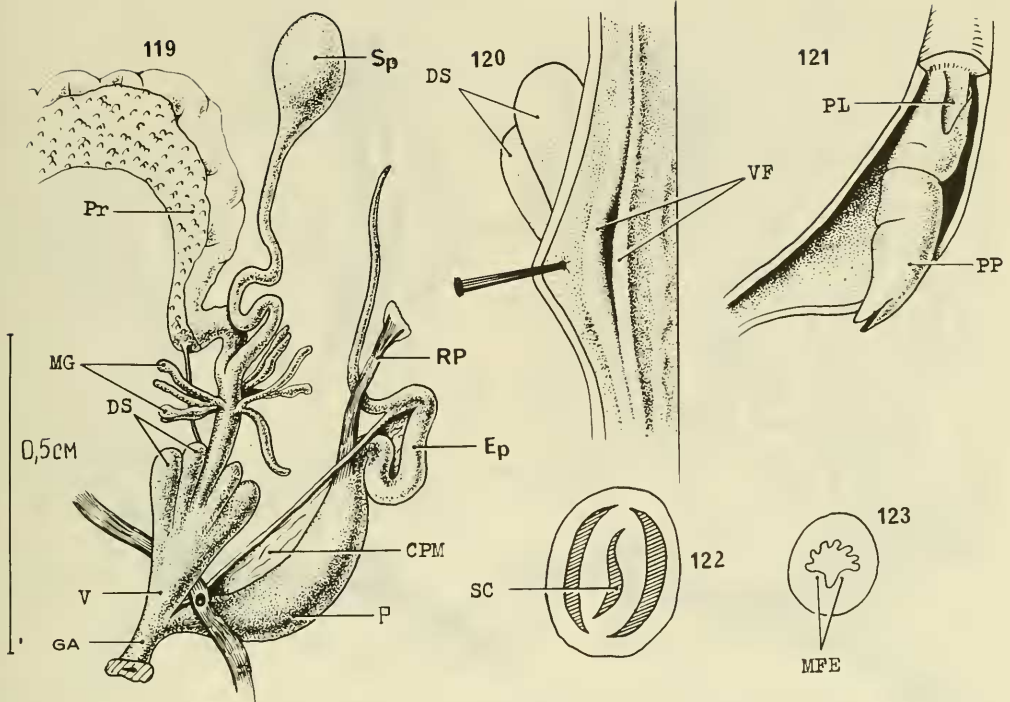
Whether the conchological distinctions on which the *Trichia hispida* species group (*T. plebeia*, including "*sericea*," *septentrionalis*, *concinna*) is based (Forcart, 1965) are justified could not be investigated here for lack of sufficient material. Two species of this group (*T. plebeia*, *T. concinna*) are discussed as separate species in this paper, although it has not been possible to determine whether the anatomical distinctions found are species-specific or just due to seasonal variation.

#### *Trichia (Trichia) plebeia* (Draparnaud, 1805)

Figs. 119-127; Pl. VII, 25, 26

Four specimens were dissected that had been collected from Grdlovez village, near Prague, Czechoslovakia, on 18 September





FIGS. 119-123. *Trichia (Trichia) plebeia* (Draparnaud), Grdlozecz village, near Prague, Czechoslovakia, 18 September 1968. 119, reproductive tract; 120, inner structure of vagina in dart sac region; 121, penis, penis sheath partly removed; 122, cross-section of verge; 123, cross-section of epiphallus.

1968 by V. Hudec and identified by him (Figs. 115-119; Pl. V, 25). Another 4 specimens originated from Bodetal in the Harz region, German Democratic Republic. These were collected in June 1969 by E. Clauss and identified as *Trichia "sericea"* (Figs. 124-127; Pl. VII, 26).

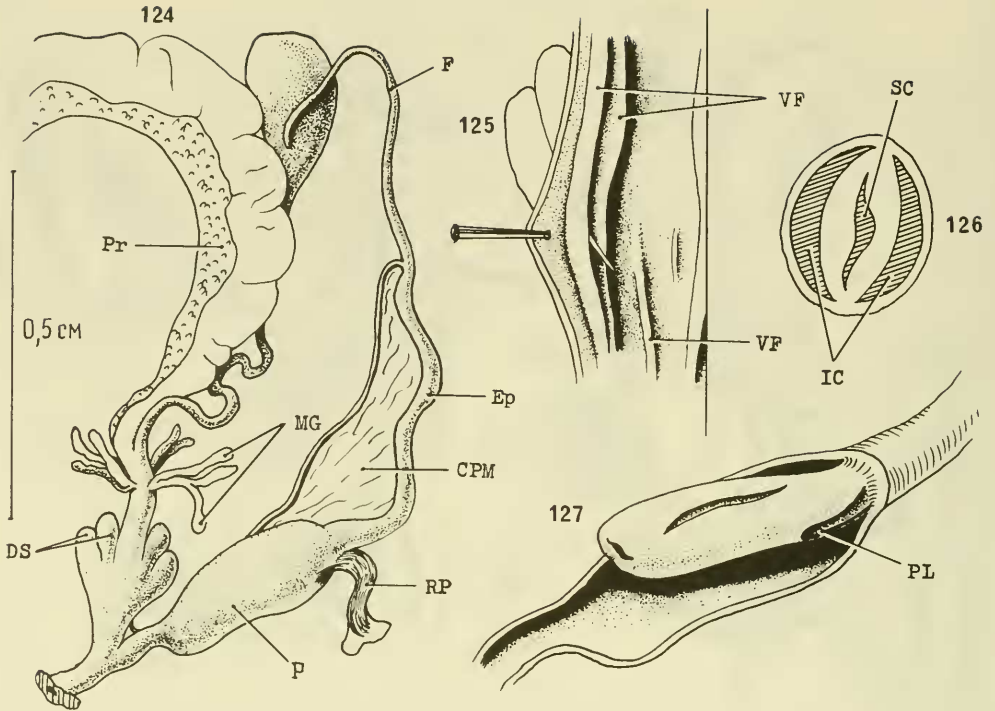
The Czech specimens are as follows: there is a smooth curve where the spermatheca continues as the free oviduct, which is also gently bent. There are 4 mucous glands, each with 2 or 3 branches. The dart sacs are elongate, opposite to one another and to the upper part of the vagina. The dart sac region is not set off but passes smoothly into a conically tapering lower vagina. The vaginal plicae are relatively well developed but form no lobes. The flagellum is about the same length as the epiphallus, which bends sharply 2-3 times; its various parts are connected by a membrane stretched between it, the penis and the vas deferens. The penis is fusiform and slightly curved. The verge is marked by a few incomplete ring grooves. The seminal duct is not

attached to the inner walls of the papilla by thin longitudinal bands but is fused to the wall at 2 diametrically opposed spots, and the 2 nonadhering sides between them constitute the 2 intrapapillar cavities (Fig. 122). The spermathecal duct is somewhat convoluted; the spermatheca is small and oval and almost reaches the albumen gland.

The German specimens agree in most respects. Note, however, that they rather resemble *T. concinna* in others, such as the unwound position of the epiphallus, which is not held in the bent state by the connective tissue membrane; the smooth outer aspect of the papilla, which lacks ringed grooves; and by the presence of short additional vaginal plicae. The spermatheca was larger in these specimens than in *T. plebeia* from Czechoslovakia and did not reach the lower edge of the albumen gland.

*Trichia (Trichia) concinna* (Jeffreys, 1862)  
Figs. 128-131; Pl. VII, 27

Four specimens were dissected. They were collected in the vicinity of Rožnave,



FIGS. 124-127. *Trichia (Trichia) plebeia* (Draparnaud), Bodetal, Harz region, German Democratic Republic, June 1969. 124, reproductive tract; 125, inner structure of vagina in dart sac region; 126, cross-section of verge; 127, penis, penis sheath partly removed.

Slovakia, Czechoslovakia, by V. Hudec on 15 July 1962 and identified by him.

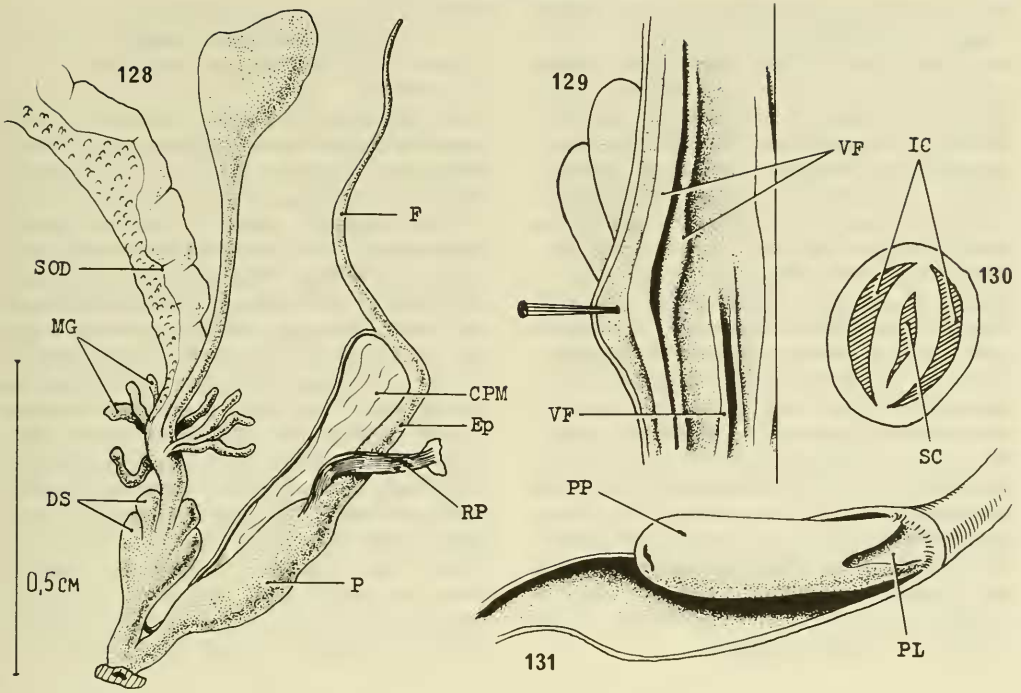
The spermatheca curves weakly at the emergence of the oviduct and at the bend of the oviduct. There are 4 mucous glands, each with 2-3 branches. The dart sacs are short and club-shaped, closely pressed together and partly fused. The dart sac regions are vaguely offset from the cylindrical vagina. The flagellum is almost 1.5 times longer than the cylindrical, weakly curved epiphallus. As in both preceding species (*T. plebeia*, *T. unidentata*), the male ducts are bound by a fine, transparent, connective tissue membrane. The verge is cylindrical or slightly fusiform, with a large papillar lacuna. The inner structure of the papilla is as in *T. plebeia*. The spermathecal duct is almost straight. The receptaculum seminis is rather bulky and irregularly shaped; it just fails to reach the albumen gland.

*Trichia (Trichia) hispida* (Linné, 1758)  
Figs. 132-137; Pl. VII, 28

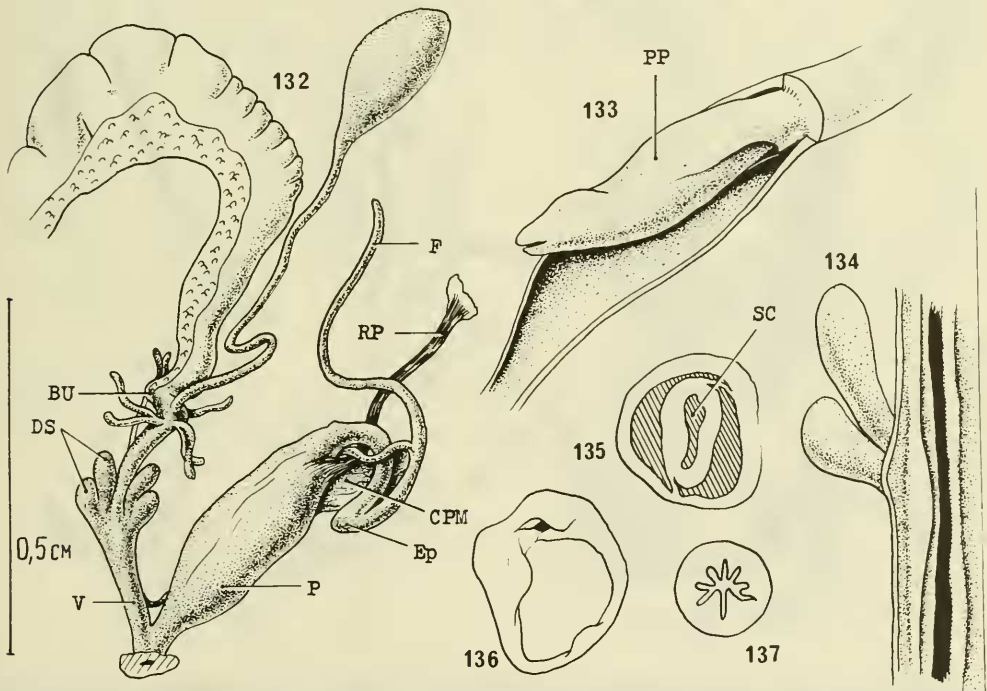
Forty specimens were examined. They were collected as follows: in the USSR, 11

specimens from the Lenin Mountains in Moscow on 12 July 1970; 13 specimens from the Ilyich Foundation settlement near the Serebryanka River, Moscow region, on 15 August 1970; 4 specimens from the garden of the Zoological Institute, USSR Academy of Sciences, Leningrad, on 28 September 1965; and 5 specimens from Stryisky Park, Lvov (Eastern Ukraine), on 25 September 1969. All these were collected and identified by me. Further, 4 specimens were collected from a garden in the town of Quedlinburg, German Democratic Republic in April 1969 by E. Clauss and identified by him. Lastly, 3 specimens from the region of Cologne, German Federal Republic, were collected by H. Nordsieck and identified by V. Hudec.

At the point where the oviduct emerges from the spermatheca, there is a smooth curve; the oviduct is also slightly bent. There commonly are 4 mucous glands, rarely 3; usually each has 2 branches but secondary branching is not uncommon, so the total number of branches may amount to 12. On the other hand, some branches may be reduced, bringing down the total to 4 or 5. The inner pair of dart sacs may be



FIGS. 128-131. *Trichia (Trichia) concinna* (Jeffreys), Rožnave, Slovakia, Czechoslovakia, 15 July 1962. 128, reproductive tract; 129, inner structure of vagina in dart sac region; 130, cross-section of verge; 131, penis, penis sheath partly removed.



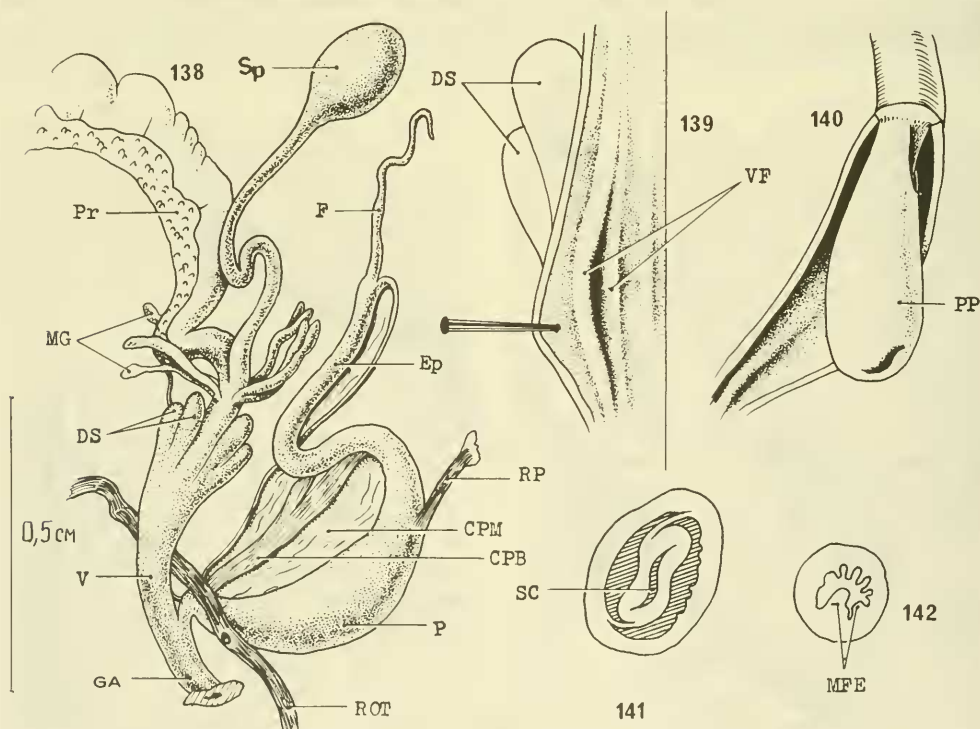
FIGS. 132-137. *Trichia (Trichia) hispida* (Linné), Lenin Mountains, Moscow, USSR, 12 July 1970. 132, reproductive tract; 133, penis, penis sheath partly removed; 134, inner structure of vagina in dart sac region; 135, cross-section of verge; 136, mantle collar; 137, cross-section of epiphallus.

developed to approximately the same degree as the outer, or they may be a little less developed. Their upper tips always considerably surpass those of the outer sacs, the mouth of the mucous glands is always considerably above the upper ends of the inner dart sacs. The lower vagina is rather long and cylindrical. The vaginal plicae are narrow but distinct. There are small lobes at the opening of the dart sacs. The length of the flagellum is equal to or greater than that of the epiphallus. Usually the latter is sharply curved and sometimes forms a loop. Between penis and epiphallus a connective tissue membrane attaches the epiphallus to the penis sheath. The penis is massive and fusiform. Its sheath is smooth inside. The verge is also fusiform. The seminal duct is more clearly separated from the papillar wall than usual; i.e., it is suspended by 2 fine longitudinal bands. The spermathecal duct is gently curving and sometimes weakly twisting. The receptaculum seminis is oval and almost reaches the albumen gland.

*Trichia (Trichia) villosula*  
(Rossmassler, 1838)  
Figs. 138-142; Pl. VIII, 29

Three specimens were dissected. These were collected from Babice, near Brno, Moravia, Czechoslovakia, on 16 August 1968 by V. Hudec and identified by him.

The oviduct makes a rounded bend. There are 4 mucous glands, of which some have 2 branches. The dart sacs are very elongate, closely opposed to each other and to the upper vagina. They are massive; the tips of the inner sacs extend beyond those of the outer sacs. Anatomically this species stands apart from others of the subgenus *Trichia* because the tips of the inner dart sacs reach the base of the mucous glands. The vagina is long, slowly narrowing to the genital atrium. The vaginal plicae are relatively well developed; they do not form lobes. The flagellum is somewhat shorter than the epiphallus, which is smoothly curving and linked to the penis by connective tissue bands in which there are muscle



FIGS. 138-142. *Trichia (Trichia) villosula* (Rossmassler), Babice, near Brno, Moravia, Czechoslovakia, 16 August 1968. 138, reproductive tract; 139, inner structure of vagina in dart sac region; 140, penis, penis sheath partly removed; 141, cross-section of verge; 142, cross-section of epiphallus.



fibers. In addition, the vas deferens, epiphallus and penis are bound together by a fine translucent membrane. The penis is fusiform and slightly curved. On approaching the genital atrium it rapidly narrows and forms a distinct bend. The verge is club-shaped, with large papillar lacuna and a wide slit for its outlet. Inside the penis sheath at the junction with the genital atrium there is a long fold. The seminal duct is attached to the papillar wall by 2 fine longitudinal bands. The spermathecal duct is thin, with an S-shaped bend. The receptaculum seminis is rounded and almost reaches the albumen gland.

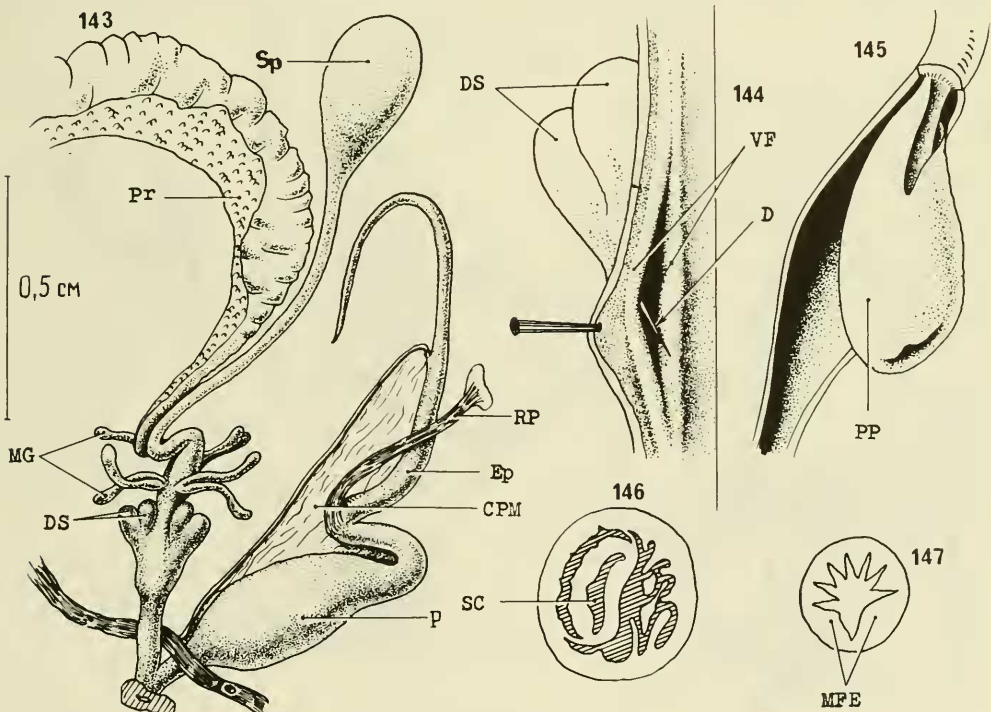
Judging from Polinski's (1924) drawings, the specimen from the town of Zakopane, Galicia, in the High Tatra region of S Poland near the Czechoslovakian border, had a flagellum approximately equal in length to the epiphallus or even a little longer. A penial band was not present.

*Trichia (Trichia) striolata*  
(C. Pfeiffer, 1828)

Figs. 143-147; Pl. VIII, 30

Four specimens were examined. They were collected in the Cologne area, German Federal Republic, on 30 May 1963 and identified by V. Hudec.

The free oviduct twice bends sharply, in the shape of an S. There are 4 mucous glands, of which some have 2 branches. Both the inner and outer dart sacs are of equal size. The inflated dart sac region is sharply offset from the thinner, lower part of the vagina. The vaginal plicae, which arise rather suddenly, do not form any lobes. The flagellum is about as long as the epiphallus or a little longer. The connective tissue membrane between the distal portions of the male duct is well developed. The penis is fusiform, massive and bulbous; the penis sheath is smooth inside; the distal



FIGS. 143-147. *Trichia (Trichia) striolata* (C. Pfeiffer), Cologne area, German Federal Republic, 30 May 1963. 143, reproductive tract; 144, inner structure of vagina in dart sac region; 145, penis, penis sheath partly removed; 146, cross-section of verge; 147, cross-section of epiphallus.

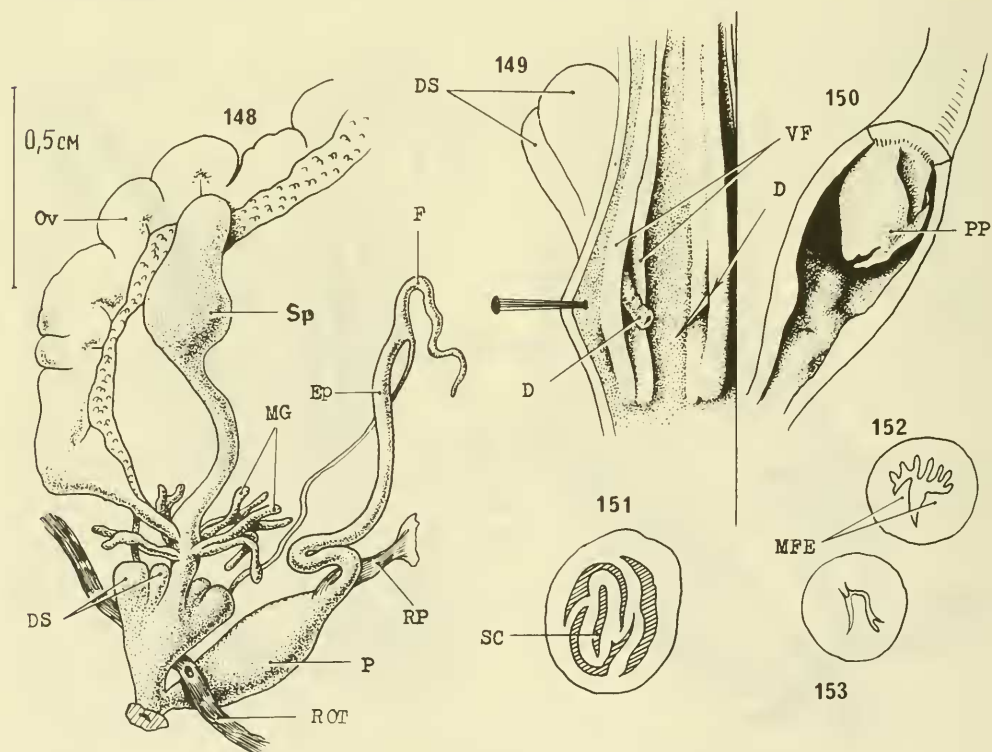
part of the penis is cylindrical. The verge is club-shaped, with a very widely split foramen and a large papillar lacuna. The seminal duct is attached to the papillar wall by 2 longitudinal bands. It differs from the other members of the subgenus in that 1 of the 2 intrapapillar cavities surrounding the seminal duct is larger than the other and has very friable, corroded walls with many hollows and lamellae (Fig. 146). The spermathecal duct repeats the bend of the oviduct in its basal part. It is thin and ends in an oval receptaculum seminis that almost reaches the lower edge of the albumen gland.

***Trichia (Trichia) danubialis***  
(Clessin, 1874)  
Figs. 148-153

Two specimens were examined. They were collected near Petržalka village, near Bratislava, Slovakia, Czechoslovakia, on 15 April 1965 by V. Hudec and identified by him.

The oviduct is straight or faintly curving. The mucous glands, originally 4, may

be reduced to 2; some of them show multiple secondary branchings. The dart sacs are well developed and massive; the outer pair is larger than the inner. The lower vagina is very short and not set off externally. The 2 pairs of vaginal plicae occupy lateral positions and abruptly stop below the mouth of the dart sac ducts and before the genital atrium (Fig. 150); they do not show any lobes. The flagellum is  $2/3$  the length of the epiphallus and is thin and curving. In its distal part the epiphallus sharply curves twice. The penis sheath has an internal longitudinal fold. The verge is short and fusiform; it occupies only the proximal part of the cavity of the penis sheath. The seminal duct is attached to the papillar wall by 2 longitudinal bands. In addition to the 2 intrapapillar cavities thus surrounding it, there is another unpaired cavity in the papillar wall (Fig. 151). The papillar lacuna is very large. The spermathecal duct is short and thick, only weakly curving. The receptaculum seminis is pear-shaped and does not reach the lower part of the albumen gland.



FIGS. 148-153. *Trichia (Trichia) danubialis* (Clessin), Petržalka village, Bratislava area, Slovakia, Czechoslovakia, 15 April 1965. 148, reproductive tract; 149, inner structure of vagina in dart sac region; 150, penis, penis sheath partly removed; 151, cross-section of verge; 152, cross-section of epiphallus near penial retractor; 153, cross-section of epiphallus in proximal part.

This species is usually treated as a subspecies of *T. striolata*, but the conchological as well as anatomical distinctions are without doubt important enough to warrant full species status. It should be noted that the photograph of *T. striolata* in Ložek's book (1956) depicts a specimen taken from the same place as the *T. danubialis* we have studied. Unless one takes these forms to be sympatric, one may suppose that Ložek's *T. striolata* is the snail here identified as *T. danubialis*.

The peculiarities of the outer morphology of the genitalia of *T. danubialis* have been previously noted by Hudec (1964).

#### Genus *Edentiella* Polinski, 1929

The shell is similar to that found in the representatives of the subgenus *Petasina* of *Trichia* but is distinguished by narrower umbilicus and by the absence of a tooth in the aperture. The mucous glands are long and rather well developed. The flagellum length is equal to the joint length of penis and epiphallus or a little shorter. The inner structure of the verge is as in the Cau-

casian *Caucasigena*; i.e., there is a system of intrapapillar cavities that are divided by longitudinal septa. The seminal duct is attached to the interior papillar wall by a single longitudinal band.

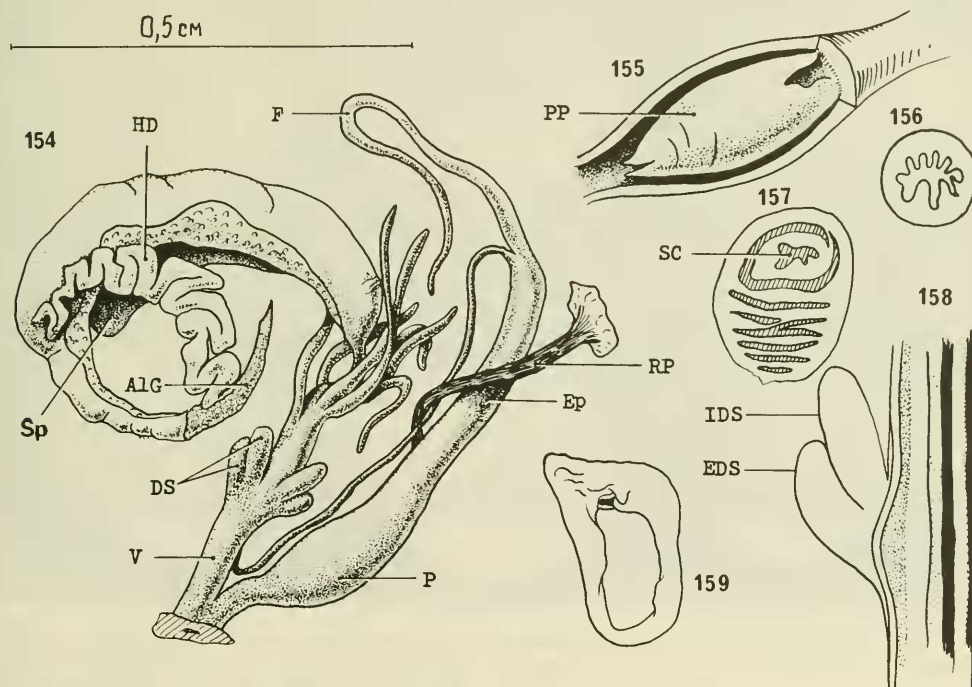
Type-species: *Helix edentula* Draparnaud, 1805.

#### *Edentiella bakowskii* (Polinski, 1924)

Figs. 154-159; Pl. VIII, 31

Five specimens were examined. I collected them in a beech forest in the vicinity of Kvasi village, near the town of Rakhov, in the Transcarpathians (Ruthenia), Ukrainian SSR on 14 September 1969, and I identified them.

As the spermoduct passes to the oviduct, it suddenly narrows and makes a slight curve. Further down the oviduct gradually widens. The mucous glands are very well developed; they are about as long as the female tract between the attachment of the spermathecal duct and the genital atrium, or a little shorter. According to my observations, the glands, usually 6-8 in number, are not grouped in bundles but are located around the oviduct at the level of the spermathecal duct takeoff. Hudec



FIGS. 154-159. *Edentiella bakowskii* (Polinski), Kvasi village, Rakhov district, Transcarpathian region, Ukrainian SSR, 14 September 1969. 154, reproductive tract; 155, penis, penis sheath partly removed; 156, cross-section of epiphallus; 157, cross-section of verge; 158, inner structure of vagina in dart sac region; 159, mantle collar.

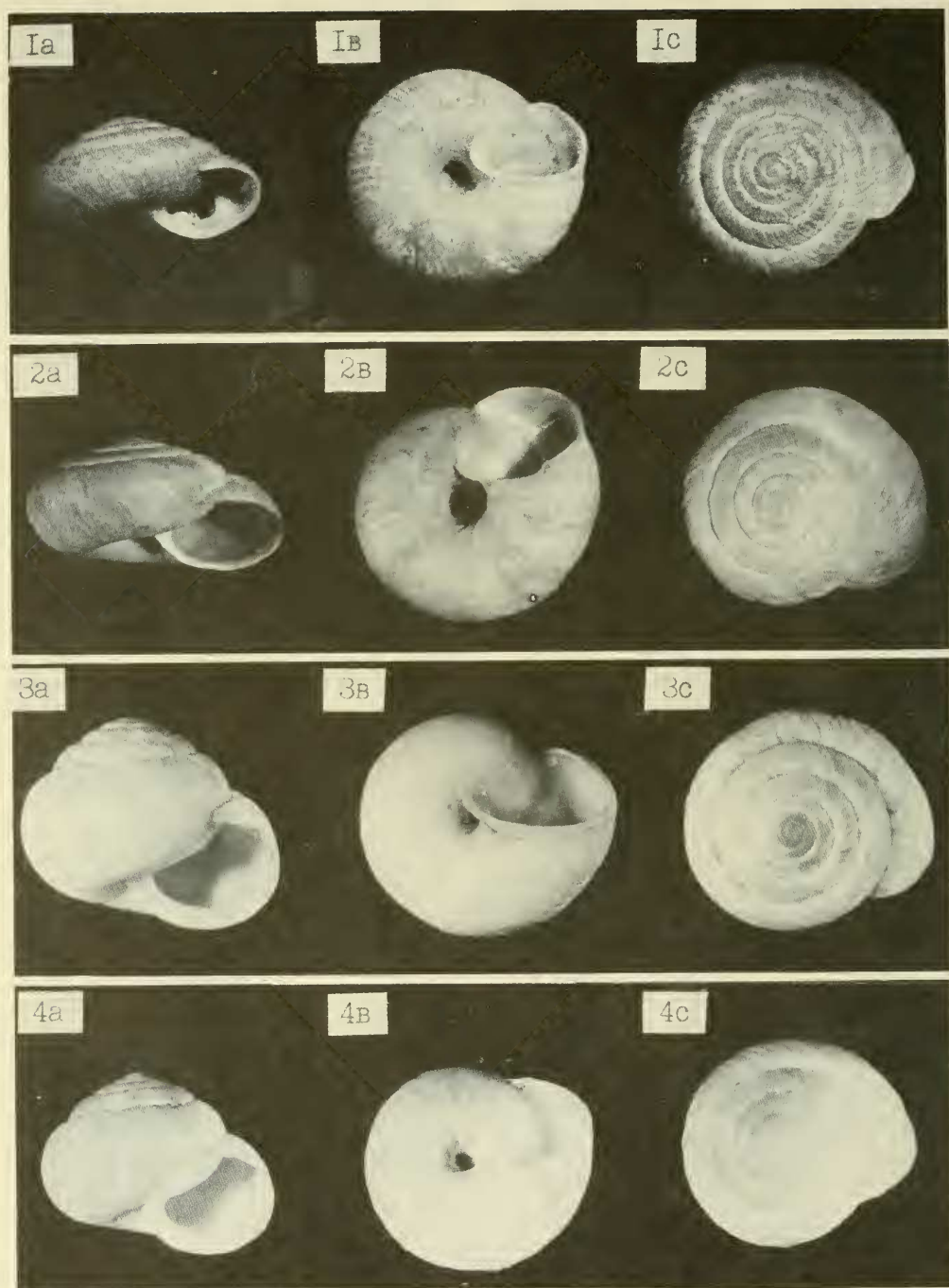


PLATE I (not actual size). 1a, b, c, *Odontotrema diplodon* Lindholm, Chatkal Range, NW Tian-Shan Mountains, Kirghiz SSR, May 1972. 2a, b, c, *Leucozonella ferghanica* Lindholm, Sary-Chileck Nature Reserve, Chatkal Range, NW Tian-Shan Mountains, Kirghiz SSR, 6 July 1966. 3a, b, c, *Leucozonella caryodes* (Westerlund), Talas Range, NW Tian-Shan Mountains, Kirghiz SSR, 4 June 1972. 4a, b, c, *Leucozonella rubens* (Martens), foothills of the Kirghiz Range, NW Tian-Shan Mountains, Kirghiz SSR, 15 June 1972.





PLATE II (not actual size). 5a, b, c, "*Euomphalia*" *regeliana* (Martens), foothills of the Kirghiz Range, NW Tian-Shan Mountains, Kirghiz SSR. 6a, b, c, *Leucozonella rufispira* (Martens), Anzob pass, Hissar Range, W Tian-Shan Mountains, Tadzhik SSR, 28 July 1968. 7a, b, c, *Leucozonella retteri* (Rosen), Kandara Valley, Hissar Range, W Tian-Shan Mountains, Tadzhik SSR, 2 July 1967. 8a, b, c, *Leucozonella caria* Shileyko, sp. nov., holotype, Khodzcha-Obi-Garm Rest Home, Hissar Range, W Tian-Shan Mountains, Tadzhik SSR, 28 May 1968.

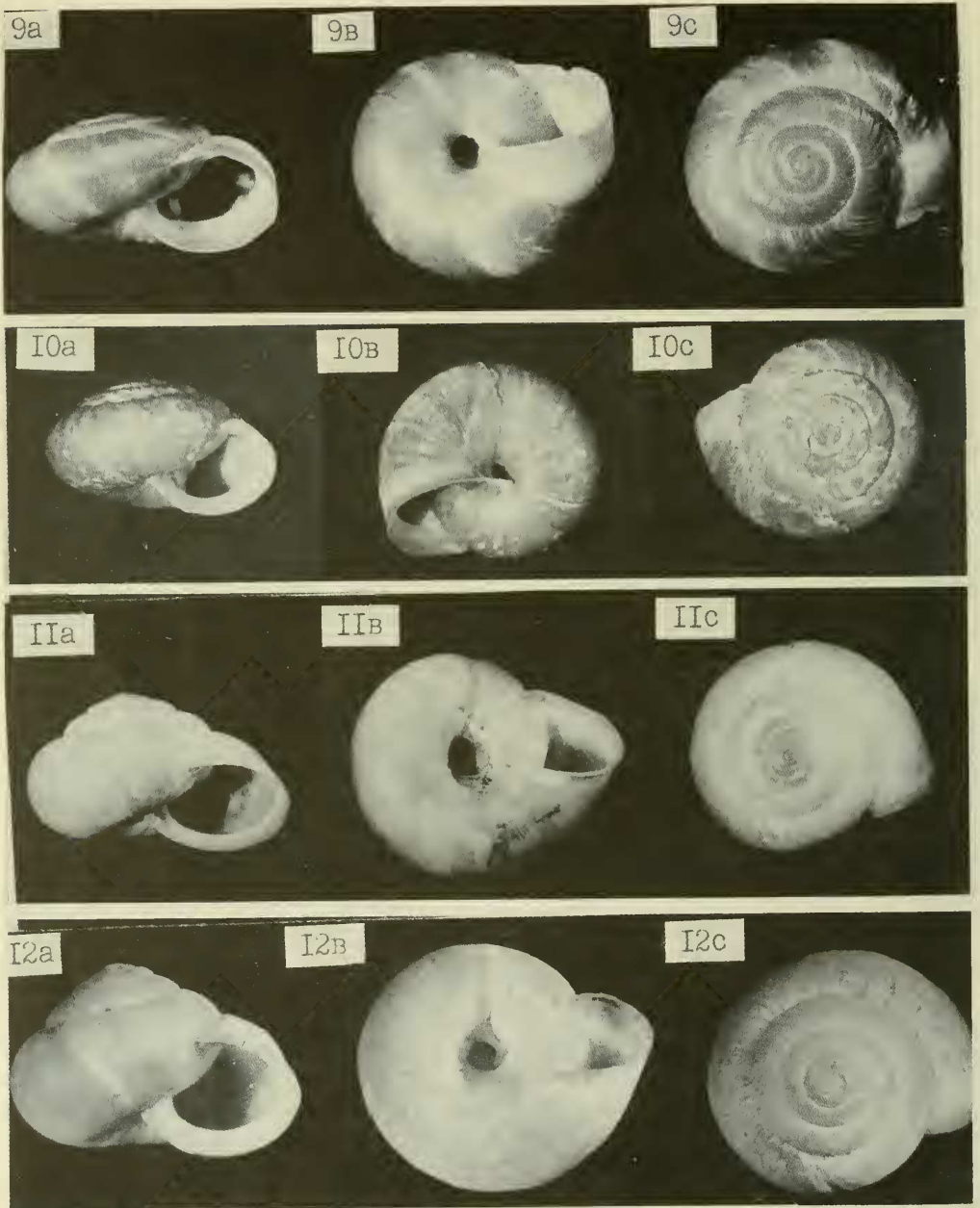


PLATE III (not actual size). 9a, b, c, *Hygrohelicopsis darevskii* Shileyko, sp. nov., holotype, Chegem Valley, N slope of central Caucasus, USSR, 10 August 1965. 10a, b, c, *Teberdinia zolotarevi* (Lindholm), topotype, Teberdia Nature Reserve, NW Caucasus, USSR, 24 July 1958. 11a, b, c, *Kokotschashvilia tanta* Shileyko, sp. nov., paratype, between Sioni and Kazbegi villages, slope of central Caucasus, Grusinian SSR, July 1969.

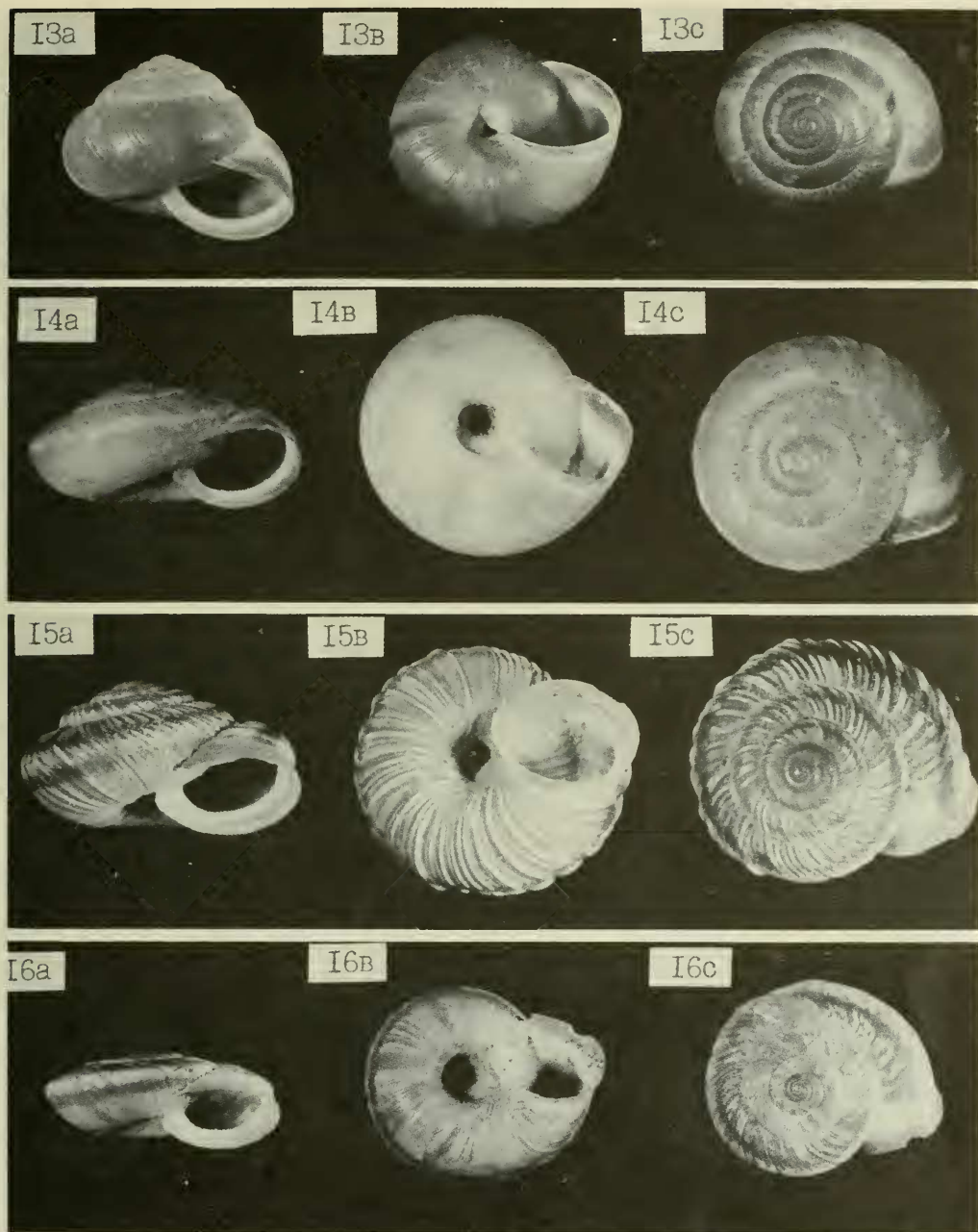


PLATE IV (not actual size). 13a, b, c, *Kokotschashvilia phaeolaema* (Boettger), Chegem Valley, N slope of the central Caucasus, USSR, 14 May 1970. 14a, b, c, *Caucasigena (Caucasigena) armeniaca* (L. Pfeiffer), Mt. Bzovdal (Mt. Todar), Stepanavan region, Armenian SSR, 18 July 1951. 15a, b, c, *Caucasigena (Caucasigena) tschetschenica* (Retowski), Kurtatin Valley, middle course of Phiagdun River, central part of N Caucasus, USSR, 19 September 1970. 16a, b, c, *Caucasigena (Caucasigena) rengarteni* (Lindholm), Khushotosyrt village, Chegem Valley, central part of N Caucasus, USSR, 14 May 1970.



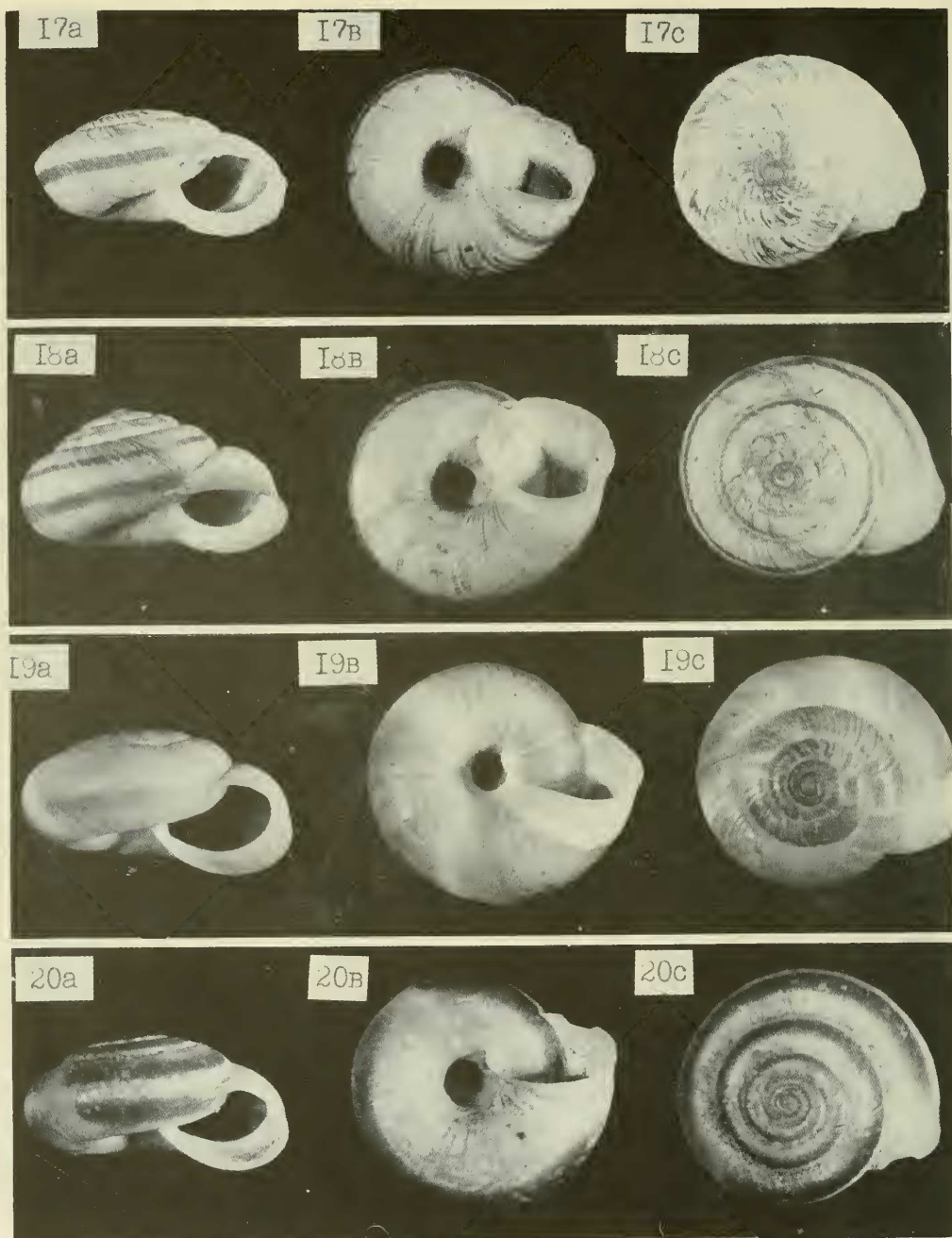


PLATE V (not actual size). 17a, b, c, *Caucasigena (Caucasigena) rengarteni* (Lindholm), old settlement of Ara-Boran, between Chegem and Baksan valleys, central part of N. Caucasus, USSR, 17 May 1970. The form described by Lindholm under the name *Helix gerassimovi*. 18a, b, c, *Caucasigena (Caucasigena) eichwaldi* (L. Pfeiffer), Chmi village, Darial Valley, near Ordjonikidze (North Osetia), central part of N Caucasus, USSR, 8 May 1970. 19a, b, c, *Caucasigena (Anoplitella) schaposchnikovi* (Rosen), old settlement of Ara-Boran, between Chegem and Baksan valleys, central part of N Caucasus, USSR, 17 May 1970. 20a, b, c, *Caucasigena (Anoplitella) schaposchnikovi* (Rosen), Chegem Valley (damp, shady slope) near Khushtosyr village, central part of N Caucasus, USSR, 15 May 1970.



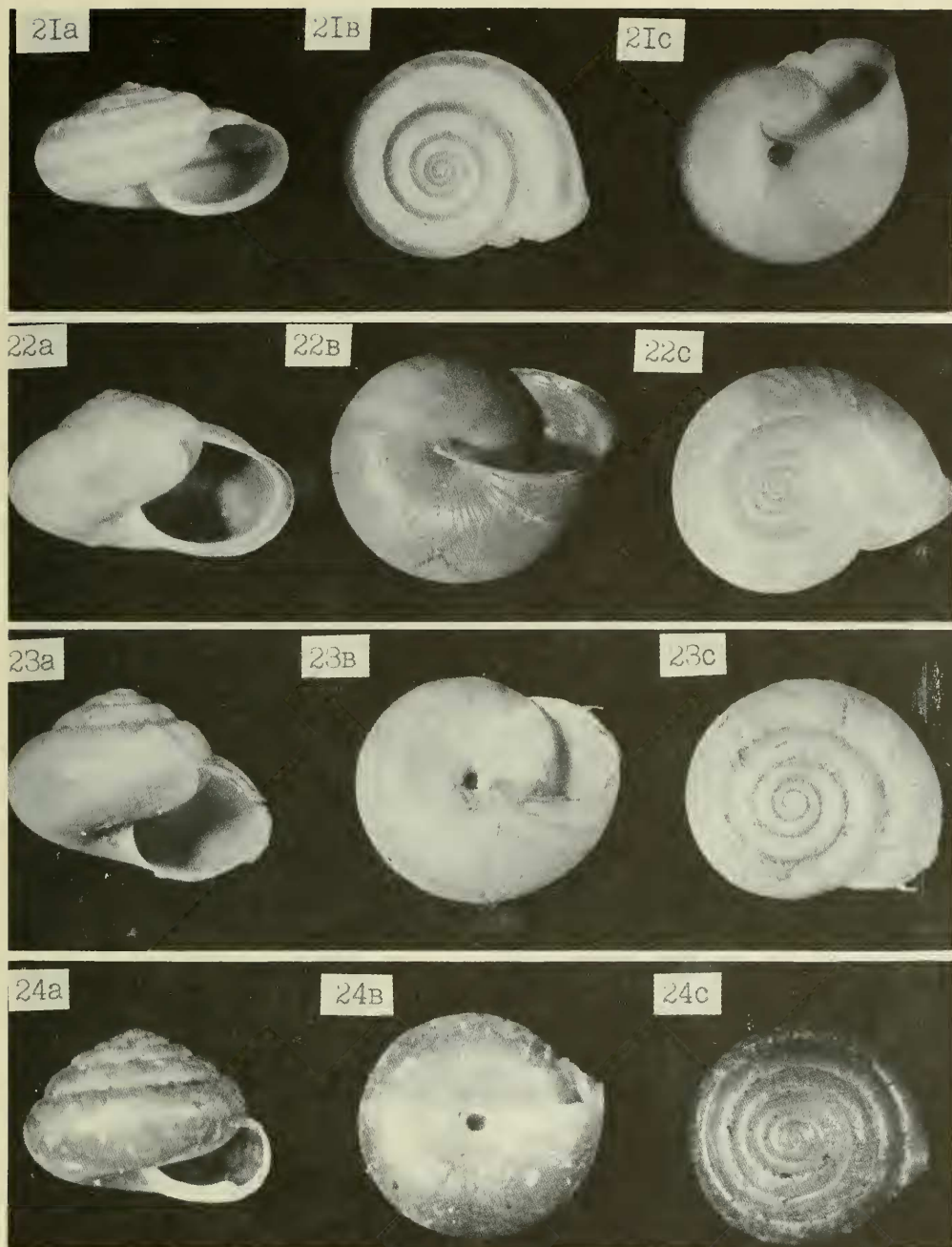


PLATE VI (not actual size). 21a, b, c, *Xerocampylaea zelebori* (L. Pfeiffer), Roumania. 22a, b, c, *Caucasigena (Dioscuria) thalestris* (Lindholm), Novy Aphon, N of Sukhumi, Black Sea region of Georgia, Grusinian SSR, 2 July 1913. Specimen not fully mature. 23a, b, c, *Plicuteria lubomirskii* (Slóssarski), Olomouc, Moravia, Czechoslovakia, 16 April 1964. 24a, b, c, *Trichia (Petasina) unidentata* (Draparnaud), central Czechia, Czechoslovakia, 8 September 1969.

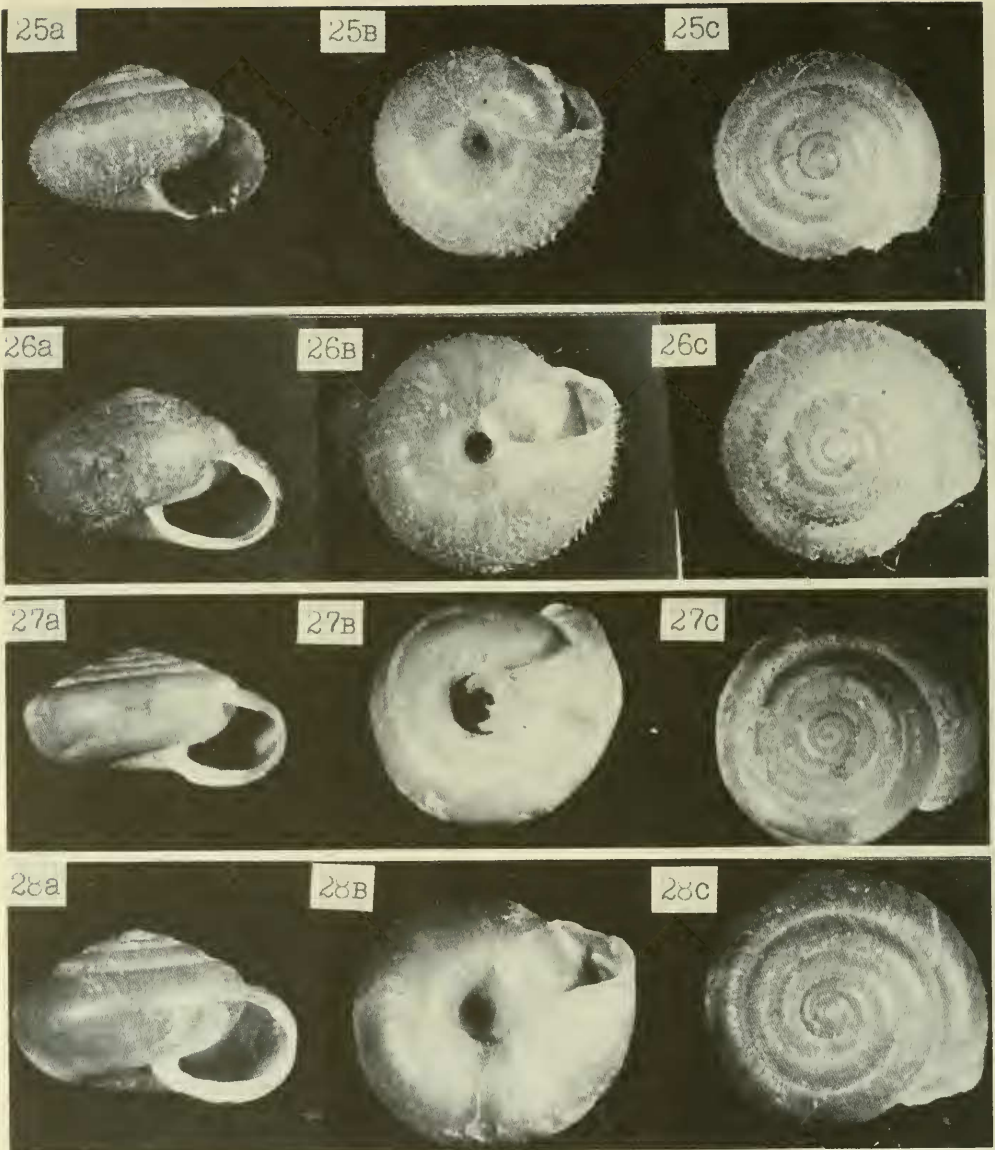


PLATE VII (not actual size). 25a, b, c, *Trichia (Trichia) plebeia* (Draparnaud), Grdlozecz village, near Prague, Czechoslovakia, 18 September 1968. 26a, b, c, *Trichia (Trichia) plebeia* (Draparnaud), Bodetal, Harz region, German Democratic Republic, June 1969. 27a, b, c, *Trichia (Trichia) concinna* (Jeffreys), Roznava, Slovakia, Czechoslovakia. 15 July, 1962. 28a, b, c, *Trichia (Trichia) hispida* (Linné), Lenin Mountains, Moscow, USSR, 12 July 1970.

(1965) notes the presence of 2 glands, each with 4 branches. Presumably these glands may either be sited independently or be grouped in 2 fascicles. The dart sacs are elongate, well separated from the upper vagina. The outer and inner pairs are developed to approximately the same degree. The lower vagina is cylindrical. The vaginal plicae are clearly formed. They may

be weakly inflated near the outlet of the dart sac ducts, but they do not form lobes. The flagellum is 1.5-2 times longer than the straight epiphallus (in Hudec's work the epiphallus is described as being curved); this organ passes smoothly into the penis without any demarcation. There is either no membrane between vas deferens, epiphallus and penis, or it is insignificant. The penis is

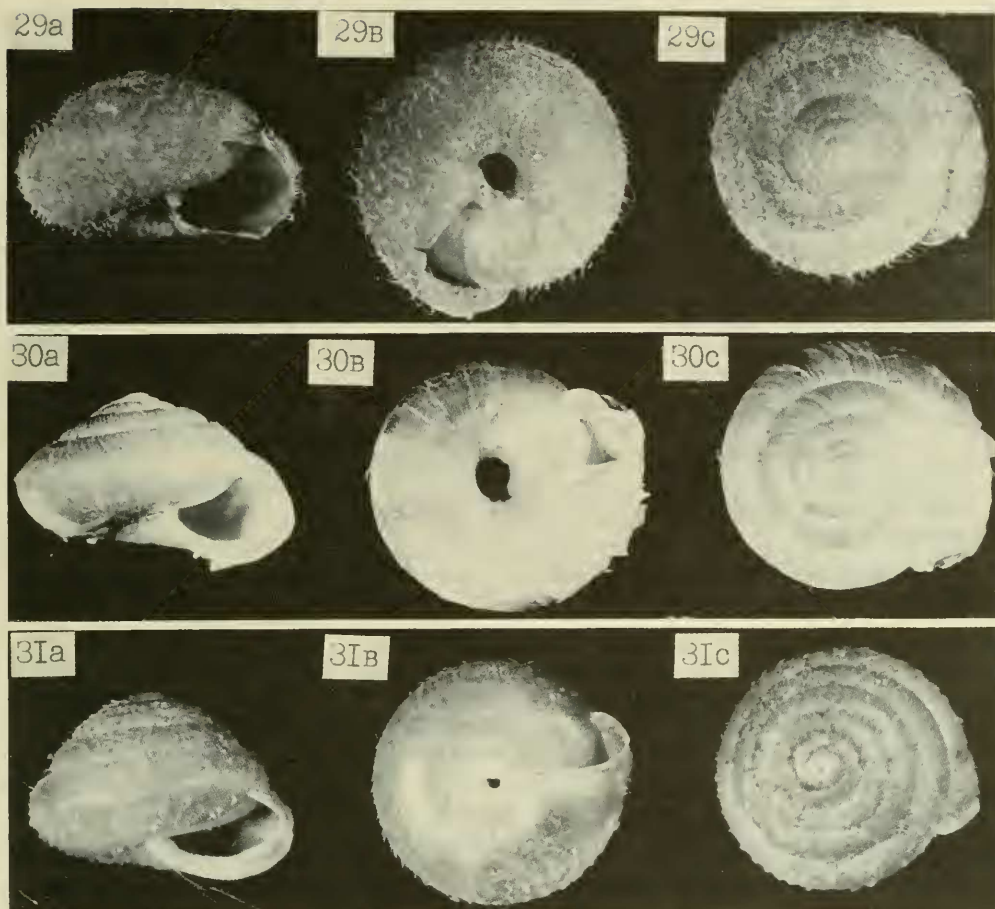


PLATE VIII (not actual size). 29a, b, c, *Trichia (Trichia) villosula* (Rossmäessler), Babice, near Brno, Moravia, Czechoslovakia, 16 August 1968. 30a, b, c, *Trichia (Trichia) striolata* (C. Pfeiffer), Cologne area, German Federal Republic, 30 May 1963. 31a, b, c, *Edentiella bakowskii* (Polinski), Kvasi village, Rakhov district, Transcarpathian region, Ukrainian SSR, 14 September 1969.

slightly bulbous; its distal part is cylindrical. The verge is perfectly fusiform. The seminal duct is attached to 1 side of the inner papillar wall by a longitudinal band; i.e., it is encircled by 1 cavity. The opposite papillar wall encloses a system of intrapapillar cavities divided by septa (Fig. 157). These more or less parallel cavities anastomose and are also all connected with the lumen of the penis sheath by the papillar lacuna. The spermathecal duct is fine and passes very smoothly to the elongate-oval receptaculum seminis, which ends quite a distance short of the lower part of the albumen gland (Fig. 154). In 1 specimen studied, the receptaculum seminis had an isolated position.

Taking into consideration the marked conchological similarity, one may suppose

that *T. edentula* (Draparnaud) and *T. bielzi* (Schmidt) [see also Soós, 1917] are close to our species. Likharev & Rammelmeyer (1952), following Polinski (1924), classify it as a variety of *T. bielzi*, noting that the dart sacs attach in the middle of the "uterus" (i.e., the part here differentiated into upper and lower vagina), which is characteristic for Polinski's section *Filicinella*. Our material, however, shows that the dart sacs are so placed in many European *Trichia*. Thus the validity of *Filicinella* becomes questionable. The final answer to this question will depend on detailed investigation of the inner structure of *T. filicina*, the type-species of this section. Note that conchologically *T. filicina* is nearer to *Trichia* s. str. than to *Edentiella*.



SHILEYKO  
IDENTIFICATION KEY

- |   |  |
|---|--|
| 1. Species inhabiting central Asia<br>Species inhabiting the Caucasus or Europe   | 2.<br>9.   |
| 2. Shell aperture with 2 teeth<br>Shell aperture without teeth  | <i>Odontotrema diplodon</i><br>3.                            |
| 3. Shell globose<br>Shell more or less depressed  | 4.<br>6.   |
| 4. Shell white, thick; body whorl lighter in color than other whorls; penis papilla without appendix near base<br>Shell horny to reddish, uniformly colored, with white spiral band; walls moderately thick; penis papilla with appendix near base                          | <i>Leucozonella caryodes</i><br>5.                           |
| 5. Shell diameter 14 mm or more<br>Shell diameter 11 mm or less   | <i>Leucozonella rubens</i><br><i>Leucozonella mesoleuca</i>  |
| 6. Shell surface with distinct periostracal hairs; diameter 9 mm or less<br>Shell surface without periostracal hairs or diameter more than 9 mm   | <i>Leucozonella caria</i><br>7.                              |
| 7. Shell surface coarsely wrinkled<br>Shell surface rather smooth   | <i>Leucozonella ferghanica</i><br>8.                         |
| 8. Shell diameter 15 mm or more, surface with spiral lines; no groove on the penis papilla (i.e., it has become closed and is now an intrapapillar cavity)<br>Shell diameter 14 mm or less, surface without spiral lines; there is a deep, open groove on the penis papilla | <i>Leucozonella retteri</i><br><i>Leucozonella rufispira</i> |
| 9. Species inhabiting the Caucasus<br>Species inhabiting Europe   | 10.<br>23.   |
| 10. Shell distinctly hirsute<br>Shell without hairs or with very short hairs  | <i>Kokotschashvilia holotricha</i><br>11.                    |
| 11. Shell with coarse, prominent radial ribs<br>Shell not ribbed or sculptured with rib-striae  | <i>Caucasigena tschetschenica</i><br>12.                     |
| 12. Shell diameter 9 mm or less<br>Shell diameter 10 mm or more   | <i>Caucasigena armeniaca</i><br>13.                          |
| 13. Shell pale greenish, with large aperture, body whorl voluminous, umbilicus minute<br>Shell does not have all features enumerated  | <i>Caucasigena thalestris</i><br>14.                         |
| 14. Shell periphery angular<br>Shell periphery rounded  | <i>Caucasigena rengarteni</i><br>15.                         |
| 15. Shell yellowish-brown, almost uniform in color; on the penis papilla there is a longitudinal groove<br>Shell color is other; penis papilla without groove   | <i>Teberdinia zolotarevi</i><br>16.                          |
| 16. Shell depressed, with washed-out radial spots; inner pair of dart sacs not visible on external inspection of upper vagina<br>Shell with more or less prominent spire; inner pair of dart sacs visible without dissection of upper vagina                                | <i>Hygrohelicopsis darevskii</i><br>17.                      |
| 17. Shell nearly globose, diameter barely exceeding the height, uniformly brown or chestnut in color<br>Shell more or less depressed, diameter markedly   | <i>Kokotschashvilia phaeolaema</i>                           |



- exceeding the height, gray or white, often with spiral bands 18.
18. Spiral bands are very faint or absent 19.  
Spiral bands are distinct 21.
19. Shell diameter 19-22 mm; in the limits of penis papilla, seminal duct attached to inner papilla wall by 2 longitudinal membranes *Kokotschashvilia makvalae*  
Shell diameter either less than 17 mm or more than 22 mm; seminal duct closely adhering to 1 side of inner wall of papilla 20.
20. Shell diameter 17 mm or less; inner wall of penis papilla with numerous plicae *Kokotschashbilia eberhardi*  
Shell diameter 22 mm or more; inner wall of penis papilla is smooth *Kokotschashvilia tanta*
21. Umbilicus is narrow *Caucasigena abchasic*  
Umbilicus is wide, perspective 22.
22. Shell rather strongly striate *Caucasigena eichwaldi*  
Shell nearly smooth *Caucasigena schaposchnikovi*
23. Shell yellowish-white, spire conical, aperture with fragile edges, almost without lip; the vaginal plicae are split into patterns of regular prismatic lamellae *Plicuteria lubomirskii*  
Shell does not have all features enumerated 24.
24. Shell of mature specimen with distinct periostracal hairs 25.  
Shell of mature specimen without hairs or with rare faint hairs 26.
25. Hairs long *Trichia villosula*  
Hairs rather short *Trichia plebeia*
26. Shell aperture with basal tooth *Trichia unidentata*  
Shell aperture toothless 27.
27. Shell perforate; wall of penis papilla contains system of cavities, separated by septa *Edentiella bakowskii*  
Shell umbilicate; wall of penis papilla contains pair of symmetrically disposed cavities 28.
28. Shell diameter 6-9 mm 29.  
Shell diameter 10-13 mm 30.
29. Shell widely umbilicate *Trichia concinna*  
Shell moderately umbilicate *Trichia hispida*
30. Shell distinctly angulate; in addition to paired intrapapillar cavities, there is a narrow unpaired cavity *Trichia danubialis*  
Shell obtusely angulated; 1 intrapapillar cavity larger than the other and with corroded internal wall *Trichia striolata*

## DISCUSSION

Analyzing the results obtained, I have concluded that the ancestral trichiae developed in 2 ways, 1 taken by the Asian forms and the other by the Caucasian-European forms.

Asian forms: by eastward migration,

some species reached the mountainous regions of central Asia. These formed shells the common shape of which is now characteristic for most of the central Asian Helicoidea (*Leucozonella*). Conchologically separate from these are *Odontotrema diplo-*  
*don* and *Leucozonella caria*, the latter strongly resembling European *Trichia* s. str.

We may assume that the verge of the initial primitive forms was a simple tube without the longitudinal groove on its surface and without any intrapapillar cavity (Fig. 160, I). In Recent Asiatic species, all the basic phases of intrapapillar cavity formation can be observed (Fig. 160, II-IV). At first the longitudinal groove on the surface of the verge is formed in the proximal part only (Fig. 160, II, *Leucozonella ferghanica*); then it extends along the whole papillar length (*Odontotrema dipledon*), deepens (*Leucozonella caryodes*; Fig. 160, III) and tends to become closed (*L. rubens*, *L. rufispira*); the final phase is the fully closed groove, which now forms an intrapapillar cavity (*L. retteri*, *L. caria*; Fig. 160, IV). In these forms the seminal duct adheres closely to the inner papillar wall on 1 side, and the intrapapillar cavity embraces it from all other sides. A remnant of the groove is the papillar lacuna that exists in all species discussed and by means of which the intrapapillar cavity connects with the cavity of the penis sheath. The circumstance that most Asiatic species have an intrapapillar cavity that remains open testifies to their relatively primitive state. This conclusion is strengthened by the fact that other Asiatic Hygromiidae are also the most primitive representatives of their groups (Shileyko, 1970).

We must further conclude that, on the whole, the "Helicidae" auct. had a wider distribution in the past than now and that recent Asiatic representatives of the group are relics from the Tertiary period.

*Caucasian-European forms*: the second path of development was the formation of 2 groups: the Caucasian and European groups. In these the formation of the intrapapillar structures evolved by another principle than in the Asiatic group. Basically, intrapapillar cavities occur in pairs in the papilla walls, embracing the centrally placed seminal duct from 2 opposite sides; the papillar lacuna forms in a parallel manner. In other words, it is necessary to assume that the papillar lacunae of Asiatic and European-Caucasian species are not homologous. Similar types of papillar structure exist in such clearly independent groups as *Hygrohelicopsis*, *Teberdinia*, *Plicuteria*, *Trichia* s. str. and in some species of the genus *Kokotschashvilia* (Fig. 160, V).

The very complex system of septate intrapapillar cavities such as are found in

*Edentiella* and *Caucasigena* (Fig. 160, IX) might possibly have formed in the way shown by species such as *Trichia striolata* and *T. danubialis* (Fig. 160, VII and VIII, respectively). It consists of the fragmentation of 1 papillar wall, in which is thus formed a tertiary cavity, i.e., a derivative of the secondary cavity, which then further disintegrates into a series of narrower cavities. Nevertheless, the totality of characters of another order makes it necessary to recognize an independent origin for the European *Edentiella* and the Caucasian *Caucasigena*.

Within the genus *Kokotschashvilia* one can observe a number of variants in papilla structure that we are here attempting to derive from the same initial point of departure (Fig. 160, V). The papilla structure in *K. makvalae* (Figs. 55; 160, V) is nearest to this initial point: the seminal duct is surrounded by a pair of intrapapillar cavities. A capillary runs in the papilla wall along 1 of the longitudinal tissue bands attaching the seminal duct to the inner papillar wall. In *K. tanta* this capillary is retained. The seminal duct is displaced toward 1 of the papillar walls and adheres to it closely; on the opposite side there still is a band of tissue separating the 2 cavities (Fig. 160, X). This division is absent in *K. eberhardi*, in which the cavity, now single, has a crescent-shaped cross-section, smooth-walled in not fully mature specimens and sinuously folded in mature specimens (Fig. 160, XI, XII). As a result, the type of papillar structure of *K. eberhardi* is formally the same as in the Asiatic *Leucozonella retteri* and *L. caria* (Fig. 160, IV). To interpret this similarity as a purely formal one is justified from 2 considerations. In the first place, the formation of the intrapapillar cavity embracing the seminal duct in *K. eberhardi* has been traced in allied species of *Kokotschashvilia* (see above). In the second place, I have made a series of dissections of *K. eberhardi* at various stages of maturity which demonstrates that in specimens not fully adult the seminal duct is still attached by a longitudinal tissue band to the papilla wall opposite to the wall it adheres to, the band dividing the intrapapillar cavity into 2 chambers (Fig. 161) just as in adult *K. tanta*.

In *K. holotricha*, the seminal duct does not adhere to the papillar wall on one side but is well removed, being held in a central position by a thin longitudinal band and

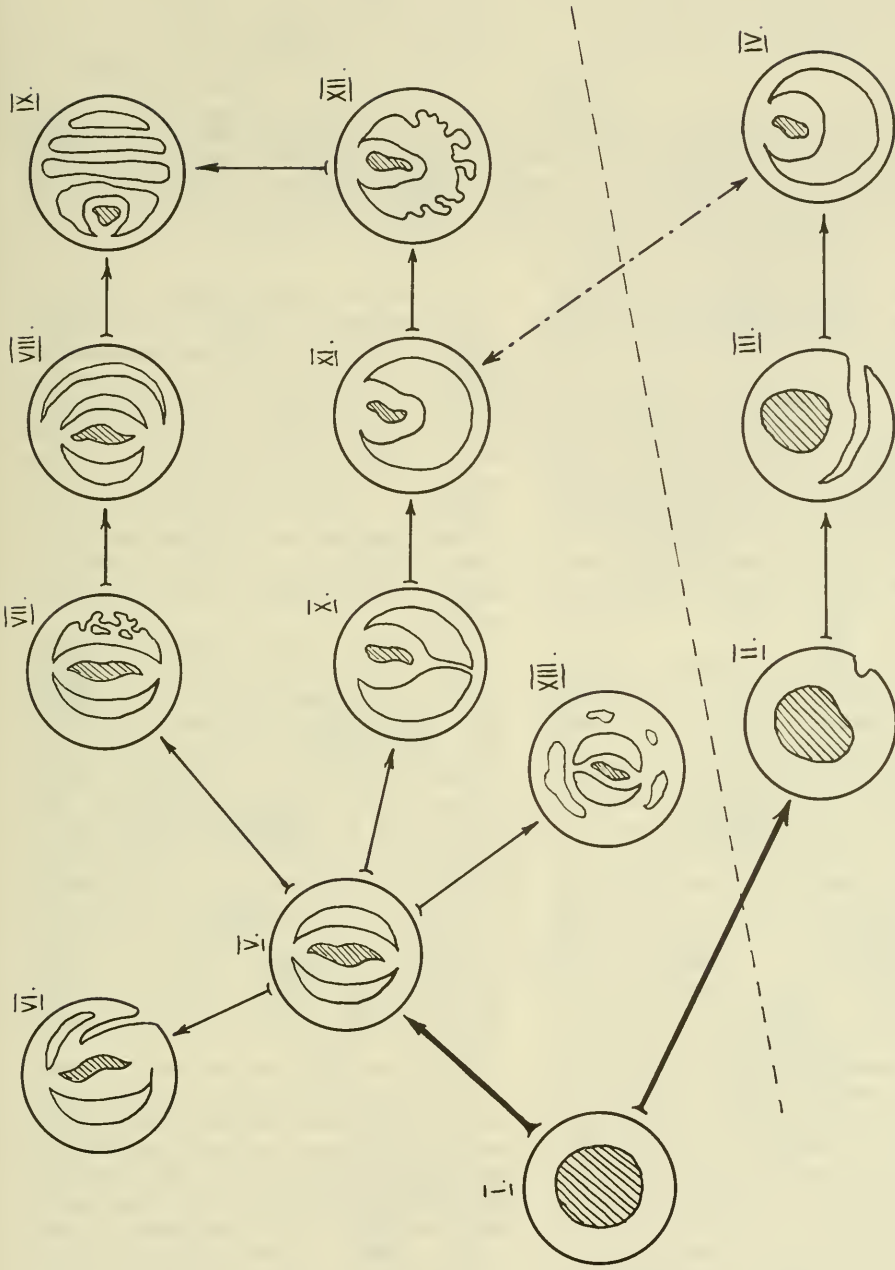


FIG. 160. Variation in verge structure in the various groups of *Trichia* s. lat. and their relationships. Cross-section of seminal duct is shaded. I, initial papilla type as a simple tube. II-IV, gradual formation of the intrapapillar cavity from a papillar groove in Asiatic species. V-XIII, various modes of formation of intrapapillar cavities from a paired cavity in European and Caucasian species, as exemplified by the following forms: I, *Leucozonella ferghanica*, distal part; II, *Odontotrema diplodon*; *Leucozonella ferghanica*, proximal part; III, *L. cariae*; IV, *L. reteri*; V, *Hygrohelicopsis darevskii*; *Plicuteria lubomirskii*; *Trichia plebeia*, *T. concinna*, *T. hispida*, etc.; VI, *Teberdinia zolotarevi*; VII, *Trichia striolata*; VIII, *T. danubialis*; IX, *Edentella bakowskii*, *Caucasigena armeniaca*, *C. rengarteni*, *C. eichwaldi*, *C. schaposchnikovi*, *C. thalestris*; X, *Kokotschashvilia tanta*; XI, K. eberhardi, immature specimen; XII, K. eberhardi, mature specimen; XIII, K. phaeolaema.

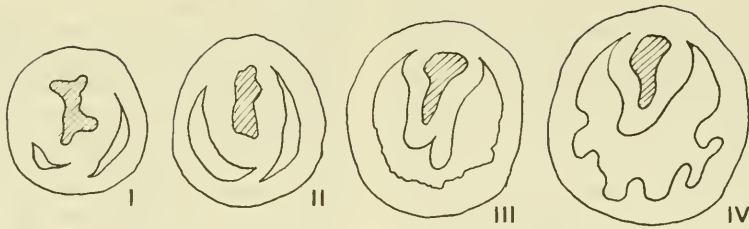


FIG. 161. Formation of intrapapillar cavity in *Kokotschashvilia eberhardi* during ontogenesis (in cross-section). I, Initial paired cavities in papilla wall and broad contact between seminal duct (shaded) and inner papilla wall. II, The cavities grow and there develops between them a longitudinal band that attaches the seminal duct to the papillar wall opposite the area of fusion with the wall. III, Connection of seminal duct and papillar wall by the band is lost by coalescing cavities. IV, Except for the one point of adherence, the seminal duct is now completely isolated from the surrounding papillar wall.

encircled by the intrapapillar cavity (Fig. 65). Finally, in *K. phaeolaema* additional sinuses have formed in the papilla wall (Fig. 160, XIII).

Just as the papillar structures in *Edentiella* (Fig. 160, IX) are derived from *Trichia striolata* and *T. danubialis* (Fig. 160, VII, VIII), those of *Caucasigena* (Fig. 160, IX) are derived from *Kokotschashvilia* in a parallel and independent manner (Fig. 160, XI, XII, IX): in *K. eberhardi* the inner papillar wall opposite to the seminal duct shows clear traces of dissolution (Fig. 70; 160, XII).

There still is 1 more variant in papillar structure: in *Teberdina* there are both a pair of intrapapillar cavities and a deep groove on the penis surface; 1 of the cavities reaches into the lobe separated off by the groove (Fig. 160, VI). At the present time it is difficult to give any comparative morphological estimation of this variant as we do not yet know any related types of papilla structure. We might imagine the formation of a third cavity from a closing groove, in which case we would get a variant corresponding to *T. danubialis* (Fig. 160, VIII). One might suppose that with the groove closing and with a simultaneous reduction of the band attaching the seminal duct to the papilla, there might arise the variant answering to *Edentiella* and *Caucasigena* (Fig. 160, IX). Assessment must be left to a later date, although the second of the modes discussed seems quite likely.

If I have paid so much attention to the details of verge structure, it is because the richness and variability of intrapapillar structures will display and reflect the common evolution of the group. No other feature offers us so rich a material for

phylogenetic reconstruction. However, while considering variants of the papilla structure in detail, I am not proposing to attach excessive importance to the characters of the papilla. The phylogenetic scheme (Fig. 162) here submitted rests as far as possible on the feature complex valuable for practical taxonomy. In the diagnosis of genera (see Systematic Part) various categories of characters are given, some of which need to be considered in discussing the proposed scheme of classification.

In addition to the anatomical features treated in connection with the Asiatic group, we shall also consider the 4 conchological types occurring in that geographical area. The first type, exhibited by *Odonototrema diplodon* (Pl. 1, 1), is very clearly distinguished by its aperture fold; the second type is the almost globose shell of *Leucozonella caryodes*, *L. rubens* and *L. mesoleuca*; third, we have the flattened shell type in *L. ferghanica*, *L. rufispira* and *L. retteri*; and the fourth is a purely European conchological type: *L. caria* (European *Trichia* are relatively small, thin-shelled, usually brown, usually hirsute).

The primitive species obviously is *Odonototrema diplodon*. Apart from the characters of the penial papilla (open groove) already mentioned, we must consider the high degree of isolation of the dart sacs. Taking into consideration the oligomerization principle of homologous organs (Dogel, 1954), and the starting point of this principle, i.e., the multiple inception of newly formed organs, we must conclude that the ancestral forms had 4 equivalent dart sacs, each of which included a dart. The first phase of oligomerization was the





loss of darts in the inner (upper) sacs. Further oligomerization of adventitious organs in the female tract causes their gradual reduction (maximal degree of reduction observed in *Hygrohelicopsis*). The presence of well-developed, clearly separated inner dart sacs approximately the same size as the outer sacs reaffirms the primitive condition of *O. dipledon*. The shell also shows the isolation of this species.

From papillar and other features it is logical to consider *Leucozonella ferghanica* to be a primitive type in respect to other Asiatic species. The groove on the surface of the verge is only weakly traced, and the upper vagina is very long. *L. caryodes* is then a derivative; the groove on the verge surface is much longer and the upper vagina less so. The shell is more globose. *L. rubens* retains a globose shape but shows reduction of the inner dart sacs and a closer connection with the surface of the upper vagina. At the same time this species has acquired a number of quite important features such as a markedly shorter flagellum, more branched mucous glands, and the presence of an intrapapillar appendix, the purpose and origin of which is not clear.

*Leucozonella rufispira*, another derivative of *L. caryodes* independent of *L. rubens*, is a distinct form by reason of other features. The flagellum length and degree of isolation of the dart sacs have not changed; the shape of the sacs has changed. The depth and general character of the papillar groove correspond to what we see in *L. caryodes*. The shell has acquired a more flattened form.

Judging mainly by the shell, *Leucozonella retteri* is a derivative of *L. rufispira*. It has a qualitatively important new evolutionary feature, i.e., the final formation of the intrapapillar cavity, but generally retains other characters of *L. rufispira*.

In the series of the central Asiatic forms, *Leucozonella caria* is prominently distinct by its shell, which, in my view, like the shells of the European trichiae, retains the initial features characteristic for the ancestral forms. At the same time the species has the essential character that relates it to the true Asiatic group: its verge structure completely corresponds to *L. retteri* (Fig. 160, IV) and has nothing to do with European species. It is necessary to point out here that study of the external

morphology of the genitalia does not engender understanding of the real essence of this species; using only the character of outer shape, we should regard *L. caria* as a member of European *Trichia* s. str., which would be very wide of the mark.

To finish the discussion of the Asiatic group, we need to point out 1 further obviously primitive feature common to all these species: the regular internal longitudinal folding of the epiphallus which, in cross-section, gives to its lumen the shape of a multiradial regular star. Subsequently 2 neighboring longitudinal folds developed more strongly while the other folds were grouped on the opposite epiphallus wall. As a result there formed 2 main spermatophore guide "rails" and a number of small ribs above them; in the furrows between these fit the rows of thorns on the spermatophore surface (Fig. 163). Such a development of the 2 longitudinal folds is observed in the Caucasian and European species. As for the Asiatic species, the differentiation of the equal folds in the epiphallus lumen is only beginning, and distinctions between these 2 groups of folds are sometimes hard to make. The lumen of the epiphallus in cross-section retains in most cases the original type of multiradial, almost regular star (see Figs. 15, 22, 32).

The European-Caucasian group of genera does not form one single developmental line, as is so well seen in the Central Asiatic forms, but is the product of some parallel and, to a certain degree, independent evolution, with the retention of a more or less definite complex of similar features. We do not find any anatomical characters permitting judgment on the evolutionary tendencies of the Caucasian and European groups. But the conchological distinctions between the European and Caucasian species are clearly seen. Generally characteristic for the European forms is a rather fragile, small- or medium-sized, usually hirsute shell of either a uniform brown color or marked with a faint white line at the periphery, whereas the Caucasian forms are, as a rule, more solid, larger, usually not hirsute and show a variety of color besides brown (chestnut, white, lilac, greenish, yellowish, etc.). There are exceptions among the European forms, such as *Plicuteria lubomirskii* and *Xerocampylaea zelebori* (L. Pfeiffer) (Pl. VI, 21). The former also stands out anatomi-

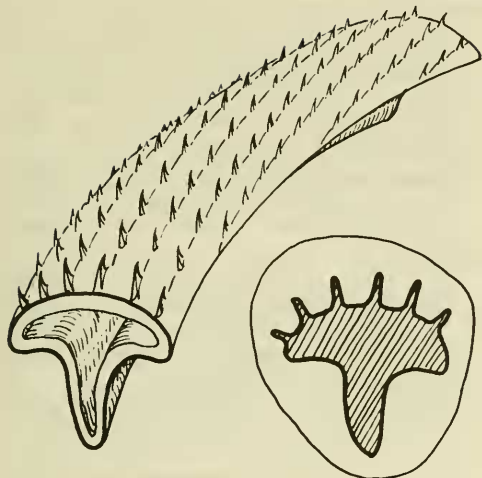


FIG. 163. Part of the spermatophore and transverse section of epiphallus (at right side) of *Caucasisigena (Caucasisigena) eichwaldi*.

cally from the general run of species. The latter is discussed below. Almost all the European trichiae are forest animals.

The Caucasian species are primarily connected with 2 types of biotope: (1) with rocks (*Caucasisigena* s. str.) and (2) with either open and dry or damp slopes (the other forms, i.e., *Hygrohelicopsis*, *Teberdina*, *Kokotschashvilia* and the other 2 subgenera of *Caucasisigena*). According to these habitats, we see 2 shell types: (1) either more or less flattened, ribbed shells, or (2) high to almost globose shells with relatively vague sculpture. The presence or absence of periostracal hairs on the shells of representatives of different species is not a constant feature: as a rule *Kokotschashvilia holotricha* almost always is hirsute; *Caucasisigena rengarteni* is generally not hirsute, but there are some specimens with short hairs. I consider the presence of hairs to be a primitive character and believe that the disappearance of this feature in the Caucasian species is an independent and parallel development.

Another conchological exception among European species is *Xerocampylaea zelebori*, a species living among rocks as does the Caucasian group of *Caucasisigena* s. str. It is now known that a rocky habitat usually produces a marked imprint on the

aspect of the shell. The conchological similarity between these forms (flat, ribbed) caused earlier authors to regard *Caucasisigena* as a separate section of the genus (or subgenus) *Xerocampylaea* Kobelt, 1871. As *X. zelebori* has not been carefully investigated anatomically, and its distribution (Serbia, in part Roumania) is quite far from the Caucasus, I do not connect these groups, particularly as I am trying to establish the independence of the genus *Caucasisigena*. Other evidence is that the shell of *X. zelebori* is otherwise quite clearly distinct from that of *Caucasisigena*; the apex is acute and not obtuse, and the contour of the whorls is not dome-shaped.

Lastly we must take into account similar features among all the species examined. Except for the presence of 2 pairs of dart sacs, the only other common character is the presence of a papillar lacuna (in species with a completely formed intrapapillar cavity), by means of which the intrapapillar cavity communicates with the cavity of the penis sheath. We assume that when the opening into the cavity of the genital atrium is closed, the increased pressure of the intrapenial liquid helps to squeeze the papilla outside, in part owing to the presence of this lacuna. In copulation the papilla is not turned inside out but is moved forward (Fig. 72). These 2 features are the only ones common to all species discussed. Even the topography of the right-hand ocular retractor, which used to be taken as the basic anatomical criterion for the assignment of any species to either the "Helicellinae" auct. or the "Hygromiinae," is not constant in the group studied. In the hygromiids living under arid conditions, the right ocular retractor passes alongside and not between the penis and vagina, and the shells of such groups have adaptive features such as very light color and strong calcification. Thus the retractor in question only passes near the distal part of the genitalia and not between them in *Hygrohelicopsis darevskii* (Fig. 42). Nevertheless, the sum total of characters of another nature (shell, penial papillar structure, pigmentation of integuments, ecology) indicates that *H. darevskii* obviously is a representative of the Trichiinae.

From the above it is clear that, for the elucidation of a true and objective system, it is necessary to enlist as many and various characters as possible. This was attempted in the present work.

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